
Mendel University in Brno
Faculty of Forestry and Wood Technology

Plant Botany

**An introduction to plant anatomy, morphology and
physiology**

Milena Martinková, Martin Čermák, Roman Gebauer, Zuzana Špinlerová

Brno 2014

Tato skripta byla vytvořena v rámci projektu InoBio – Inovace biologických a lesnických disciplín pro vyšší konkurenceschopnost, registrační číslo projektu CZ.1.07/2.2.00/28.0018. za přispění finančních prostředků EU a státního rozpočtu České republiky.



Translated from the Czech edition "Kolařík et al. (2010) Péče o dřeviny rostoucí mimo les - II." published by ČSOP Vlašim.

Translated by Ing. Roman Gebauer Ph.D. and Mgr. Lucie Novotná

Authors ´ contribution:

Milena Martinková (Chapter 1, 2, 3, 7 and 8)

Roman Gebauer (Chapter 4)

Martin Čermák (Chapter 5)

Zuzana Špinlerová (Chapter 6)

Author of figures - Milena Martinková (author of figures 9, 14, 15, 16, 18, 20 and 21 is Roman Gebauer)

Contents

1	Introduction.....	3
1.1	Life domains and phylogeny of tree growth on Earth.....	3
1.1.1	Prokaryote.....	3
1.1.2	Eukaryote.....	4
1.1.3	Evolutionary history of vascular plants.....	4
1.1.4	General characteristics and types of trees.....	6
1.1.5	What are the benefits of trees?.....	8
1.1.7	Tree reaction on the unfavourable condition.....	9
1.1.8	Ontogeny of tree growth.....	10
1.1.9	Dynamic of tree activity.....	12
2	Plant Cell.....	13
2.1	Membrane complex, semi-autonomy organelles and cytoskeleton.....	14
2.2	Nucleus.....	15
2.3	Cell ontogenesis.....	16
3	Tissues.....	18
3.1	The origin of primary meristem.....	20
3.2	Primary meristems.....	21
3.3	Permanent primary tissues.....	23
3.3.1	A system of primary surface tissues.....	23
3.3.2	A system of primary basic tissues.....	24
3.3.3	A system of vascular tissues.....	25
3.4	Secondary meristems.....	25
3.4.1	Cambium.....	25
3.4.2	Phellogen.....	28
4	Roots.....	30
4.1	The origin of root.....	30
4.1.1	General characteristics of root systems in trees.....	31
4.2	Root functions.....	33
4.3	Root zone activity (primary growth).....	33
4.3.1	Meristem zone of the root primary growth.....	33
4.3.2	The elongation zone.....	34
4.3.3	Differentiation zone.....	34
4.4	Secondary growth and root functions.....	36
4.5	Mycorrhiza.....	37
4.5.1	Vesicular-arbuscular mycorrhiza (VAM) = arbuscular mycorrhiza (AM) ...	38
4.5.2	Ectomycorrhiza (EM).....	39

4.5.3 Ectendomycorrhiza.....	39
4.6 Metamorphoses of root	40
4.7 Limiting factors of root system growth and functions.....	40
5 The stem.....	42
5.1 Secondary growth of stem	43
5.2 Development of annual rings	44
5.3 Wood of coniferous species	45
5.4 Wood of deciduous species	46
5.5 Stem morphology	47
5.6 Bud.....	49
6 Leaf.....	51
6.1 Phyllogenesis – the evolution of a leaf.....	51
6.2 Ontogenesis – the individual development of a leaf.....	51
6.3 The arrangement of leaves on a stem.....	53
6.4 The outer structure of assimilation leaves.....	54
6.5 The inner leaf structure	56
6.6 The inner needle structure	60
6.7 Evaluation of foliage state	61
6.8 Leaf metamorphoses	61
7 Propagation and reproduction of woody plants.....	61
7.1 Means of reproduction and types of diasporas.....	62
7.1.1 Artificial vegetative reproduction.....	62
7.2 Plant life cycle and the significance of seeds in phylogenesis of plants.....	63
7.2.1 Dissemination by diasporas of a generative type	64
8 Basics of woody plant physiology	71
8.1 Photosynthesis.....	72
8.1.1 The impact of exogenous and endogenous factors on photosynthesis	75
8.1.2 CO ₂ exchange in plants.....	76
8.1.3 Photosynthesis and respiration.....	77
8.2 Respiration.....	77
8.2.1 The process of respiration - oxidation of glucose	79
8.2.2 Factors of respiration.....	81
8.3 Photorespiration	82
8.4 Water regime of woody plants.....	83
8.4.1 Water content and its thermodynamic state.....	84
8.4.2 The movement of water in a cell.....	86
8.4.3 Water saturation deficit.....	87
8.4.4 Water potential of plants.....	87

8.4.6 The uptake and conduct of water	87
8.4.7 Release of water by plants	91
8.4.8 Water balance in a plant.....	96
8.5 Mineral nutrition of woody plants and the significance of nutrients.....	96
8.5.1 Roles of individual nutrients.....	98
8.5.2 Ion relations	99
8.5.3 Nutrition disorders	100

1 Introduction

If we wish to grow a plant we should perceive it in relation to its position in the vegetation system—it informs us on the stage of development in the long history of life on Earth. Moreover, we should be aware of its **demands on the environment** (i.e. environmental requirements), the degree of adaptability to changes in the environment, sensitivity or resistance to insect, fungal and other pathogens. We should be informed about the **natural extension** of this taxon on Earth (whether it is a native species or naturalized with us, or a newly introduced species, with which we lack experience) and also the **origin of its direct ancestors** (whether they are individuals originating from seed, clones or grafts). Simply put, you need to **understand each plant grown in time and space** and, what is more, as these are living organisms, we should take into consideration their **life experience and reactions**—absolute and relative age (i.e. ontogeny stage) and their growth rates and changes in shape.

1.1 Life domains and phylogeny of tree growth on Earth

Life on Earth is composed of unicellular and multi-cellular living systems (organisms capable of performing all life functions and information flow). Cellular systems originate in one hypothetically assumed ancestor called **progenot**, which evolved in two evolutionary lines about **3.5 billion years ago**. One directed to the bacteria (Prokaryote) domain and the second to the Eukaryote domain.

1.1.1 Prokaryote

Bacteria and archaea domains are unicellular organisms of prokaryotic type. Their cells contain cytoplasm, plasma membrane and **nucleoid**. Nucleoid is **not divided** from the cytoplasm **by a membrane**; it is composed of one, generally a **circular, double-stranded piece of deoxyribonucleic acid (DNA)**. The interior of these cells is **not divided** by a system of **membranes (mitochondria and plastids are missing)**. Prokaryotic organisms are capable of **heterotrophic** nutrition (as saprophytes and parasites growing both in the aerobic or anaerobic environment) as well as **autotrophic** nutrition (chemo- or phototrophic). They include species producing methane, species **tolerant of high temperatures** (up to 113 °C), high pressure, **salt** and **acid** environment. They have a relatively large surface contact with the environment, a rapid exchange of matter and energy and the fastest metabolism (generation time, i.e. the time at which parental generation gives rise a new generation, may only take 30 minutes, they are able to synthesize up to 15 amino acids in one second). **They make up about one half of the biomass (living matter) of the world.**

There are typically 40 million bacteria cells in a gram of soil and a million bacteria cells in a millilitre of fresh water. They live in water, in bodies of other organisms, and can spread through the air. They are mainly found in the **soil**, where they take part in **mineralization of remains of plant and animal bodies**. Through the decomposition of their proteins ammonia is released, and ammonium salts are then oxidized by nitrifying bacteria into nitrites and nitrates, and these are the source of plant nutrition. Some nitrogen-fixing bacteria such as *Azotobacter* and *Rhizobium* are involved in the nitrogen cycle by binding to their proteins and nucleic acids of atmospheric nitrogen. *Azotobacter* lives and fixes nitrogen independently of other

organisms. On the other hand, *Rhizobium* fixes nitrogen after entering root nodules of legume plants. Conversely, denitrifying bacteria deprive soil of nitrates and nitrites as they reduce them to molecular N₂.

Bacteria are also involved in the carbon cycle, the source of carbon dioxide (CO₂). CO₂ is released into the atmosphere by the oxidization activity of organisms (respiration of plants, animals, fermentation of chemoheterotrophic bacteria). The released CO₂ is a source of carbon for all photoautotrophic organisms, especially in the subkingdom Viridiplantae – green plants. Another element whose cycle is affected by the bacteria is sulphur. Sulphur is contained in many proteins in plant and animal bodies. Saprophytic bacteria release sulphide from their residues utilized by phototrophic sulphur bacteria as a source of hydrogen. Sulphur is then oxidized to sulphate by chemoautotrophic bacteria, which is available to plants. **Green plants are of a fundamental importance to heterotrophic consumers as essential primary producers of organic matter.**

1.1.2 Eukaryote

The most evolutionarily advanced organisms belong to eukaryotic domain, whose **minimum building unit**, capable of all **basic life functions**, is a **eukaryotic cell** – i.e. cell where the information molecule **DNA** is localized in the **nucleus** enclosed by a membrane. The most important evolutionary branches include eukaryotic **protozoa** and **chromista** such as soil organisms, **fungi**, **animals** as **heterotrophic** organisms and **plants**, mainly as producers of organic matter, i.e. **autotrophic** organisms.

1.1.3 Evolutionary history of vascular plants

Once plants had reached the land, there were two approaches to dealing with desiccation. The **bryophytes** avoid it or give in to it, restricting their ranges to moist settings, or drying out and putting their metabolism "on hold" until more water arrives. **Tracheophytes** resist desiccation: they all bear a waterproof outer **cuticle layer** wherever they are exposed to air (as some bryophytes do), to reduce water loss, but—since a total covering would cut them off from CO₂ in the atmosphere—they rapidly evolved **stomata**, small openings allowing for the gas exchange. Tracheophytes also developed **vascular tissue** to aid in the movement of water within the organisms and moved away from a gametophyte dominated life cycle. Vascular tissue also facilitated upright growth without the support of water and paved the way for the evolution of larger plants on land.

1. Cooksonia, Rhynia and Psilophyton are the first known **vascular plants** (Tracheophytes). They lived from the upper Silurian to early Devonian (443–393 million years ago) and they were **leafless** and **rootless** plants consisted of stem tissue which branched along an axis. Their bodies already had an epidermis with **stomata** and these vascular plants had ingeniously invented a chemical called **lignin** that toughens the walls of plant cells. The earliest documented plant of this type is *Cooksonia*, but a complete fossil material was not found yet. On the other hand, complete fossils were found for *Rhynia* plants. The axes of *Rhynia* exhibit a maximum **diameter of 3 mm** and the plant probably attained a height of up to **20 cm**. *Psilophyton* is a genus with more complex structure than any other plants of comparable age (e.g. *Rhynia*) and is thought to be part of the group from which the

modern ferns and seed plants evolved. *P. forbesii* is the largest documented species of *Psilophyton*. Reconstructions suggest that they were around **60 cm** tall and equipped with more advanced type of tracheid. However, no species of this family reached tree growth because of isometric growth (i.e. almost uniform in all directions), which would not be functionally and mechanically sustainable in larger sizes.

2. Pteridophytes (clubmosses, horsetails, ferns and progymnosperms) is group of vascular plants where diploid **sporophyte** (with a double set of chromosomes in the cell nuclei) **predominates over gametophyte**, which is haploid (with one set of chromosomes) in individual lives. **Trees** (with a minimum height of 4 m and diameter of 7.5 cm – measured at breast height, i.e. 1.3 m above ground) appeared for the first time in the history of Earth flora between the middle and late Devonian (350 million years ago). Since then they have been gaining in size in all dimensions, mainly in the stem diameter. The earliest known trees originated in the *Wattieza* genus. At those times, lush and dense vegetation spread in **humid habitats**, while dry habitats with a low ground water only had a sparse vegetation cover. The plants growing in wet habitats were competing for light and this selective pressure was responsible for the evolution (phylogeny) of tree habitus. The tree-high growth was discovered independently, but more or less at the same time in ferns (*Pseudosporochnus*, *Calamophyton*), clubmosses (*Protolpidodendropsis*, *Cyclostigma*), horsetails (*Pseudobornia*) and progymnosperms (*Eospermatopteris*, *Archaeopteris*). At the same time tree plants, especially progymnosperms, (genus *Duisbergia*) occurred in **drier**, sparsely populated **habitats**, too. In this case, the **tree growth was advantageous in terms of improving bioclimate** in the crown (to avoid temperature fluctuations near the soil surface) and in terms of ability to limit water loss (due to massive solid trunk, which also served as a reservoir of water and other substances). Furthermore, trees had an advantage of producing high-quality organic matter (mineralization of dead tree parts brings nutrients back into the soil in the most favourable ratio and form for a particular species), **long life and slow population growth**, which was an asset to sustaining stability in an individual as well as the whole forest. Yet, trees could appear in evolution only after satisfying their **basic living need**. It needed sufficiently **developed and deep soil** in order to provide a tree with solid anchoring and covering of their needs for water and mineral nutrients.

3. Gymnosperms plants (conifers, cycads, *Ginkgo*, seed fern and *Gnetales*) as a group of seed-producing plants appeared in the Palaeozoic Devonian 405–345 million years ago. They have an **imperfect protection of ovules** that grow **freely on scales**. These ovules ripen into seeds. Pollen is transferred directly onto the naked ovules. Male and female micro and megasporophylls usually form separated male and female cones. The pollination by wind occurs. Seed ferns are an extinct group of plants with tree or liana structures, large pinnate leaves resembling fern leaves. **The most primitive group of present seed plants are Cycads**, nowadays found in tropical and subtropical areas reaching about 130 species. A class of *Ginkgo* originated in late Paleozoic and gradually spread to a large areal of the Earth. In the Tertiary (65–2.5 million years ago), however, most *Ginkgo* species died out, and only a single species – *Ginkgo biloba* survived till present flora. The first **conifers** have been known since the Carboniferous period (345–280 million years ago). Their greatest era was the Mesozoic (252–66 million year ago). At present coniferous forests cover approximately one third of all forest ecosystems area.

4. Angiosperms (Flowering plants – *Magnoliophyta* – **dicots and monocots**) appeared at the end of the Mesozoic in Late Cretaceous (140 million years ago).

Angiosperms differ from their predecessors by the position of **ovules inside the carpel** (gynoecium), **enclosed seeds in fruits and stamens with carpel** that are usually protected by colourful **corolla**, which attracts pollinators. Angiosperms offsprings of the Cretaceous era are found nowadays in tropical and subtropical areas (myrtle, *Magnolia* or *Liriodendron*). In higher latitudes, this group is represented by mild climate species, such as willow, oak, birch, beech. The **treelike monocot species** do not have a continuous and full wood stem cylinder; **stem grows as a set of leaf petioles and sheaths** with a possible coappearance with adventitious roots. Conductive systems are built from closed vascular bundles, which are composed of xylem and phloem. The xylem typically lies adaxial with phloem positioned abaxial.

1.1.4 General characteristics and types of trees

The **prerequisites** for the existence of trees do not only include the **capability to build a functional multicellular organism** (e.g. vascular architecture), but also to **synthesize the necessary construction, storage, defence and regulatory substances**. These include accumulation of the storage and other substances into the cells (starch, proteins, fats or substances of the defence system – anthocyanins, tannins, dyes, aromatic and bitter substances, saponins, glycosides, alkaloids or metabolic waste products – crystals of calcium oxalate and calcium carbonate etc.), into the cell walls (cellulose, hemicellulose, pectin substances, cutin and other high molecular weight waxes, lignins, suberin, polysaccharide mucilaginous substances etc.) or into specialized locations (resins, essential oils, latex, gum, rubber and many others).

Woody plants are **perennial plants whose woody stem lives for at least two growing seasons** (e.g. raspberry, blackberry), but usually longer, i.e. from **many years, exceptionally up to thousands of years**. Woody plants are studied by **dendrology** (from Greek: dendron – meaning a tree; logia – science or study). However, dendrology does not cover the whole part of the system (unlike the case of mycology – that studies exclusively fungi), since a lot of systematic units include both herbs and woody plants (e.g. within the *Ranunculaceae* family fig buttercup *Ficaria verna* is a typical herb and old man's beard *Clematis vitalba* is a woody lian or within the genus of *Sambucus* there is a herbaceous species dwarf elder *Sambucus ebulus*, while individuals of elderberry *Sambucus nigra* grow as woody plants – shrub or tree. Moreover, there are a number of herbs able to build woody stems strong and solid enough and lateral branches that structurally correspond to woody species (wormwood, *Atriplex*, hops) – but these species are not considered as trees, since their above-ground systems die in the same year as they originate.

Woody plants – ***Plantae lignosae*** – are perennial plants with woody above-ground and root systems, exclusively adapted to the terrestrial environment. They can be divided into **Holoxyles**, whose stems **lignify in the same growing season** as they elongate, and **Hemixyles**, whose stems **fully lignify only as late as the following season** (i.e. in autumn their apical parts are still herbal pendant as they lack strength; such as blueberry). If an unligified part is damaged in rest season, this does not present a grave loss to a plant. The opposite is true – if it survives, a hemixyle has an advance when the photosynthesis starts at the beginning of the next growing season. According to a plant design (physiognomy), woody plants can be distinguished as **trees** (a distinct **main trunk remaining unbranched** in its lower part (the height may vary depending on the species and conditions from just a few cm such as seedlings

or bonsai to more than 100 m), **shrubs** (higher than 0.8 m not developing a distinct main trunk, with the **stem branching of its basal part above or below the soil surface**).

Trees have a large, extensive root system, which passes into a compact, space-minimized (intense) and clearly established trunk near the soil surface. A trunk branches at a certain height above the ground and carries a crown. The crown usually grows in its periphery, i.e. in height and width and the stem can be found either around full length (e.g. spruce), or it may soon form strong, numerous skeletal branches (as solitary broadleaf).

Shrubs, woody cushion plants and creeping woody plants also have extensive above- and below-ground systems, but do not build a trunk—they develop new and stronger branches from the lower buds, i.e. close to the soil surface. Shrubs with a root system covered in the soil are known as chthonophytes. Above-ground parts of woody cushion plants also have a nearly hemispherical shape with dense, short shoots around the surface. The surface of such a compact unit is relatively small related to the volume of the occupied space—such a shrub is thus protected from temperature fluctuations and drying out. Above-ground parts of creeping woody plants are pressed against the surface of the soil (e.g. cotoneaster) and the ends of branches may be ascending.

Epiphytic shrubs grow on other plants, usually trees (epiphytes can also be currant, yew tree and a number of other species and such trees as rowan or maple growing on other trees and generally not forming a trunk in these unfavourable conditions). They do not harm the host plant if there is enough space in the crown or if the host plant falls and the epiphyte plant reaches the soil surface. Though, typical tropical and subtropical epiphytes may outgrow a host tree and kill it (strangler).

Hemiparasitic shrubs such as yellow mistletoe and European mistletoe are connected with their host plants directly by haustoria; they prosper in the top, sunlit part of a tree crown, where their green leaves produce organic matter to their own use (**Fig. 1**). They **withdraw solutions from the host species** that were obtained with a great energy lost from the soil and pulled up against the force of gravity. These shrubs often have a spherical shape whose surface is ideal for capturing solar radiation and reducing excessive water loss by evaporation into the air.



Fig. 1 Oak branch infested by yellow mistletoe (*Loranthus europeaus*). The branch top part dyed as nutrients and water were taken by mistletoe.

Woody lianas can be divided into several types:

- **entwine** – their stems perform rotational movements at their apices, which serve to wrap around a support. Later they grow, get thicker and can graft among coils – e.g. Dutchman's pipe (*Aristolochia macrophylla*), Chinese wisteria (*Wisteria sinensis*)
- **prop** – often shortened reverse stems or emergencies – prickly outgrowths of bark, which hold lians on the substrate. E.g. blackberry (*Rubus fruticosus*)
- **with tendrils** – such as grapevine (*Vitis vinifera*)
- **with tendrils** with suction pads, as Japanese ivy (*Parthenocissus tricuspidata*)
- **with aerial rootlets** with matted pads – form as adventitious roots on stem without absorption function, such as English ivy (*Hedera helix*).

Material and energy investments are dedicated to their **linear extension growth and efficient transport system** (connecting leaves with roots) over long distances (e.g. *Calamus ratang* reach a length of up to 300 m). **Stems lack self-supporting systems** and they are dependent on the support plant in reaching the irradiated area. Sometimes lians are also referred to as skeleton parasites, that is when they climb as high as the crown of a bearing tree, overshadow it and let the tree gradually die.

1.1.5 What are the benefits of trees?

A large volume of occupied soil gives them a **better chance** of getting the necessary **amount of water and mineral nutrients**; they can accumulate storage substances of organic nature, water and nutrients in their bulky bodies so that they could **overcome unfavourable periods** for growth. The lignified stems (branches and trunks) carry **reserve buds** which can easily replace lost crown parts (damaged by frost, drought, wind, fire etc.). A vast **foliage area is produced very quickly** at the beginning of the growing season, which is an advantage over herbs in the use of solar radiation for photosynthesis – this also extends the growing season. Reaching an area of faster airflow and milder temperature fluctuations makes their **reproductive structures better protected**; they can also utilize **air movement for propagating pollen and diaspores** (fruits, seeds and shoot fragments capable of rooting, such as crack willow – *Salix fragilis*). All growth forms of woody plants support the development of large forests and bushes. **Cooperative relations** between individuals (e.g. by root grafts, mutual shading, creating favourable temperature and humidity conditions, mitigating the damage by wind etc.) together with **competitive relations** (competition for water, nutrients, oxygen and symbionts in the soil, the favourable irradiance above the soil surface) are run in plant societies (corresponding to certain environmental conditions). In this context trees can reach ages and sizes close to the species potential optimal. **Trees are the most demanding growth form**. In unfavourable conditions many tree species shift to a shrubby form when they grow old.

1.1.6 Disadvantages of tree growth and possible solutions

The main disadvantages of trees are **high demands on supply by photosynthates** that arise in green parts of plants (especially in leaves, but also in petioles and young stems). These green parts must produce enough energy to cover needs of the extensive growth of the below- and above-ground systems, the annual creation of new, functional conductive pathways and mechanical and static stability of the organism and for securing covering tissues to new and growing tree surfaces. Photosynthates are also needed for the synthesis of materials, construction of

defence structures, forming osmoregulatory substances, symbioses investment (mycorrhizal fungi) and for making their own storage supplies for survival periods of dormancy and resuming growth in spring. Adult trees also have increasing demands for security of generative (sexual) reproduction, i.e. the formation of flowers, fruits and seeds. In all these conditions **foliage of trees works at a much lower level of hydration than the herbs or low shrubs do**. This is because the driving force for transport from roots to leaves (i.e. water potential difference between these two points) in trees must be large enough to overcome any resistance that may occur on the long flow pathway of water from the soil to the atmosphere. The **growth and stability** of a tree depends largely on the **vulnerability of the "thinnest place" – stem**.

The conductive and mechanical systems of a stem are oversized several fold in healthy individuals, but material and energy input into the structure of a tree cannot be reused even in the condition of a critical starvation. Many tree species are able to reach the **"optimal design" in unfavourable conditions**, which means to **exclude a stem**, recover branches from the stem base, shorten the distance between leaves and roots, reduce the demands of the water regime, in other words, to shift from the tree growth to the shrub growth. We can seldom encounter the opposite direction – rejection of the injured stem, so that the roots grow from the base of the crown (e.g. under bark or through the hollow in the stem) towards the soil. Thus, the support and storage functions of the stem are partially replaced and at the same time the resistance of solutions movement is reduced on the way from soil-plant-atmosphere system.

Slow wood production together with a reduced speed of the radial growth of branches (branch overhanging) are other **tree strategies** leading to efficient energy balance.

1.1.7 Tree reaction on the unfavourable condition

Tree species as long-living plants do not live only under favourable conditions for their existence, growth and reproduction. Large **energy demands** are required by a tree to overcome unfavourable conditions and stress, which cannot be just escaped from by trees physically as they are immobile organisms with fixed root systems in a particular area. **The process of disturbance and reaching a new equilibrium** takes place at the level of cell membranes and organelles, and it extends to individual cells, plant tissues (especially meristematic, photosynthetic and conductive) and individual organs (e.g., leaves, roots). Finally, it also concerns whole individuals, i.e. autonomous elements of the ecosystem (whether natural or artificial). At first, there is a **stress stimulus**, whereupon a **stress response** is triggered. By the term "stressor" we understand the factors of external or internal environment that cause the organism threat to its functional relations. The **stress response** is a **change of the functional status** (e.g. bent branches for light absorption – phototropism, diversion of branches and their growth from consistently irritate subject – tigmotropizmus, remodelling or termination of elongation growth of roots in compacted soil and restoration of root growth in a more positive direction, etc.).

The outcome of the stress response, which individual tree species are equipped with, regarding the conditions of the areas of their original extension may include:

- a) avoiding the effects of the stressor** (e.g. inner leaves, especially auxiliary buds of woody cushion plants are hidden from temporary drought and heat)
- b) adaptation**, which means adapting of sensitive structures so that it **can withstand**

the effect of the stressor – (e.g. the sunlight leaves with modified inner structure, carried on short branches in clusters are more tolerant to repeated insufficient water supply)

c) resistance to a certain extent of a stressor, i.e. achieving resistance (for example vegetative buds of conifers and deciduous trees can resist freezing -90 to -196 °C in the areas with long and tough winters; in the short summer this resistance is missing).

These examples are known as **eustress**, which is a stress essential for life, **a driving force of changes leading to the ability to live in a given environment** (even optimal).

The failure of a stress response, i.e. the destabilization or even death of an individual is caused by one or more conditions, the sum of whose is known as **distress**. It is the **destructive effect** of the impact to a sensitive taxon. Stress response goes through certain stages. **The alarm stage** is the pledge of all existing functions, in particular the synthesis of various agents and growth restriction. Affected tissue respire heavily and break the existing structure – **catabolism predominates over anabolism** (but spiral shock may spin and cause acute damage and death – such as peripheral parts of leaves due to salt or bleached districts in immature leaf blades due to intense solar radiation, etc.)

The restitution stage could follow, resulting in the **correction processes** of protein synthesis and protective substances or even replacing the lost parts by a new growth. Regularly repeated stressors during phylogeny of a species are preceded by plant precautions, the hardening stage. During this stage the components of cell membranes are substituted, osmotically active substances are released to free water to avoid the formation of ice crystals, etc. **Trees can achieve resistance by gradual preparation** (see above). Sometimes a **chronic injury** can be observed in cases when changes and changing stressors occur irregularly. A range of stress responses are nonspecific. On the cell level changes in the enzyme activity (reductases: glutathione, peroxidases), biosynthesis of polyamines and antioxidants (ascorbic acid and tocopherol), the type and content of the osmoticum (proline, betaine and polyol), the synthesis of secondary compounds (polyphenols, anthocyanins, terpenes), synthesis of stress hormones (abscisic acid, jasmonic, ethylene), changes in the properties of membranes, increased respiration and decreased photosynthesis. **The result of the changes in the relationship between respiration and photosynthesis** (i.e. increasing the proportion of ADP/ATP) **is the depletion of the trees** and the lack of promptly available energy. The production of biomass is reduced (living matter), growth irregularities and reduced fertility occur (poor internal coordination of growth results in the allometric relation changes between production, photosynthesizing and consumption parts), and, furthermore, a tree gets old prematurely (increased necromass – dead matter of crown, stem, roots). **Internal factors** that determine the susceptibility or resistance of trees to a given stressor or complex of stressors, are: a **taxon and eco-element** (i.e. shady, sunny, xerophyt, mesophyt etc.), **ontogenetic stage, dormant stage or stage of vegetation activity**.

1.1.8 Ontogeny of tree growth

Tree growth, no matter which evolutionary branch it applies to, can be characterised by the following conditions:

- a) **trees must be mechanically stable** (energy to grow and support structures is provided by leaves),
- b) **aqueous solutions of the nutrients must be** received mainly from the soil and **quickly transported** to the leaves,
- c) **organic materials** – products of leaf synthesis – **need to be conducted fast enough and in required quantities** to the shoots, flowers, fruits, branches, stems and roots
- d) all parts of tree need to have a sufficient available **storage space for water, nutrients and storage substances**.

These characteristics are essentially **contradictory** as **all conditions must be met and all require energy**. Thus, the **resulting structure and shape** of the plants is their **compromise**. This compromise may be reached in the ontogeny, i.e. in the development of individuals from seedlings to adult trees by these means:

- **root system, stem and crown develop simultaneously** – such as spruce, beech – tree appearance is preceded by the **initial phase**, i.e., roots and leaves develop while the stem grows in diameter. Only after achieving the required foliage area and soil occupancy the trunk will elongate (especially ferns, cycads, some angiosperm species that lack the so-called secondary growth – such as palms),
- a **dense root system** is formed close to the soil surface, i.e. at the tree base, a **false trunk is formed by intense branching** (extinct ferns and present polycormons palm trees)
- **epiphytes** living in crowns of host trees, too, may present the initial stage of trees ontogeny. They let aerial roots down to the soil surface that gradually grow thicker and stronger, thus forming a stem, which expands in the soil into an independent root system (some species of the genus *Ficus*)

Ontogenetic stages can be divided in **two periods: the dependence stage** – the period when a young plant uses the reserves stored from the endosperm or cotyledons (A), and the **independence stage** – when photosynthesis has become active (B):

A. heterotrophic period, the individual's life depends on photosynthates supplied by the parent plant, namely:

1. seed stage and germination

B. autotrophic period, when the new plants can produce and process their own organic inputs for their growth and development

2. germination (since the full function of the first assimilation leaves)

3. juvenile stage (it is typical for example in thin Norway spruce needles still undifferentiated into the shady and sunny type)

4. virginal stage (tree habitat is similar to the adult tree, but still does not flower or give seeds and fruits)

5. stage of younger adulthood (from the first bloom). It should occur after the achievement of the required range of the stock compartment. In fruit and ornamental trees it occurs before they reach 10 years; if the vegetative propagation or grafting was used, it can emerge even much sooner. Domestic forest trees bloom at the age of several decades, i.e., after an almost final volume of the crown is reached. A repeated strong stressor, such as undercutting and lateral contraction of roots in nurseries, could promote early flowering in these trees.

6. stage of middle adulthood (mean maximum crown and root space is reached and quality seeds are produced)

7. stage of late adulthood (rounding or downsizing top of the crown with monopodial branched species, reducing the amount of crown, dieback of deep roots and a gradual transition to flat root system)

8. senescence stage (prevalence of necromass over biomass, reduced fertility, reduced seed germination)

9. stage of senility (tree survives by a few branches associated with a narrow strip of cambium with partly living roots)

10. death of the individual

Trees are **highly sensitive to stress factors in the younger ontogenetic stages**. However, **they adapt most efficiently** to their environment just in these stages. Many seedlings live or at least survive on very unfavourable sites. On the other hand, the shock from transplanting from a nursery, where seedlings were growing in the optimal conditions (fertilization, irrigation, soil aeration, etc.) into the environment dramatically different and unfavourable (compacted soil, changes in temperature, humidity, light condition) can meet the tree species unprepared. This could lead to numerous and repeated plantings mortalities. **At the end of a tree life** (from late adulthood), its adaptability is reduced and **sensitivity to changing and frequent occurrence of stressors increases**.

1.1.9 Dynamic of tree activity

During the long life of trees rhythms and long term cycles of **increased and decreased activity get repeated**. The **shortest rhythm is daily (circadian)** and is associated with changing light and dark parts of the day. In the light part photosynthesis should prevail and towards the end of the night, when trees may have the greatest water content, intense volume growth of cells should occur. Some sensitive plants demonstrate **a monthly, the circa-lunar rhythm**, which is related to the increasing and decreasing moonlight intensity. The activity of most species of our flora is clearly subject to an **annual cycle (cycle circa-annual)**, i.e. changes due to the change of seasons – spring, summer, autumn and winter, when the driving factor is the temperature.

The daily rhythm depends on the proportion of the **length of day and night**, i.e. on the **photoperiod**, whose changes are related to the annual cycle. In our latitudes the light part of the day extends from the spring equinox to the second half of June with the longest day and shortest night. Then, the night gradually lengthens and by mid-July the nights get colder (i.e. change **termoperiodicity – temperature difference between hot day and cold nights**). In the second half of September the length of day and night is equal (autumn equinox) and then the night lengthens until December. Since the end of December till March the light is on the increase again.

Many of our trees are already at the stage of cold enforced rest (post-dormancy) in the early **spring part of the annual cycle**. It depends on the weather conditions development, especially on the **last freezing days in February**. If February is warm, some trees (poplar, birch) would already begin the activity of their roots or flower buds (hazel). Many trees and shrubs bud and bloom in April, gradually moving to the stage of full vegetation activity (June, July, exception is for example lilac, which already declined to an internally controlled dormancy at that time). Shortening the length of the light part of day, cooling at night and typical weak rainfall result in trees accumulation of substances that limit cell division and growth, accelerate fruit ripening and leaf senescence and finally cause falling leaves in the internally controlled hibernation – deep dormancy. It is not a rule that summer weather is

favourable for tree species every year. Plant drying (**hydroperiodicity**) may occur in weaker rainy years and at higher temperatures. Trees may respond to drought by **early calming of their growth initiatives**, the forced rest, pre-dormancy. In a more favourable year, it often happens that even species for which such behaviour is unnatural begins **blooming again** (Horse Chestnut – *Aesculus hippocastanum*), for which a considerable amount of energy is lost. Trees **released from deep dormancy**, are driven by internal **phytohormonal relations** (in particular the level of abscisic acid – ABA) by the action of frost temperatures and higher insulation (i.e. condition, which decay ABA). Unlike most deciduous trees, *conifers* (e.g. Norway spruce) **lack internal control** and only have an imposed rest.

Also during the annual cycle **periods dangerous** to trees may be identified. It is mostly in **spring and autumn**, i.e. the **transitional period**, in which the likelihood of fluctuating temperatures is high. **Late frosts** in spring damage young shoots, or worse, lateral meristems of trunks and branches. In autumn, **early frosts** may occur when the trees have not "ripen" yet the late part of the annual rings (completed lignification of summer wood). **The highest sensitivity is in the period of a rapid growth**. Trees are most resistant during their dormancy, a time of minimised metabolism and energy exchange with the environment. Transpiration flow is interrupted, water content, movement and metabolism are reduced and growth is interrupted.

2 Plant Cell

Eukaryotic cell, such as the **minimum structural, functional and reproductive unit**, is an open system with the target behaviour of **autoregulation and autoreproduction**. This means that it grows, respirates, makes internal movements, exchanges substance, energy and information with the environment and responds to them, rebuilds and newly creates its own structure and gives rise to a daughter cell during the lifetime. This ability depends on:

- **its internal memory** – inherited and carried out according to the needs;
- **the compartmentalization** – dividing of its interior by a membrane
- **the cytoskeleton**, which is involved in the internal movement.

Living cells form a **protoplast**, consisting of the **cytoplasm** (cytosol – colloidal solution of water, protein, fat, saccharides), **complex membranes, organelles, nucleus, vacuoles and ergastic substances** produced by cell activities (crystals, rubber, oil, resin) (**Fig. 2**). A growing cell builds the **cell wall** on its surface that may be part of the inner skeleton of plants (sclerenchyma) or its vascular system (tracheids, vessels) after the death of protoplast. **Not all plant cells build the cell wall**. These include: **gametes, sexual cells**, i.e. the female (ovule cell) and male (pollen generative cells) which fertilize together.

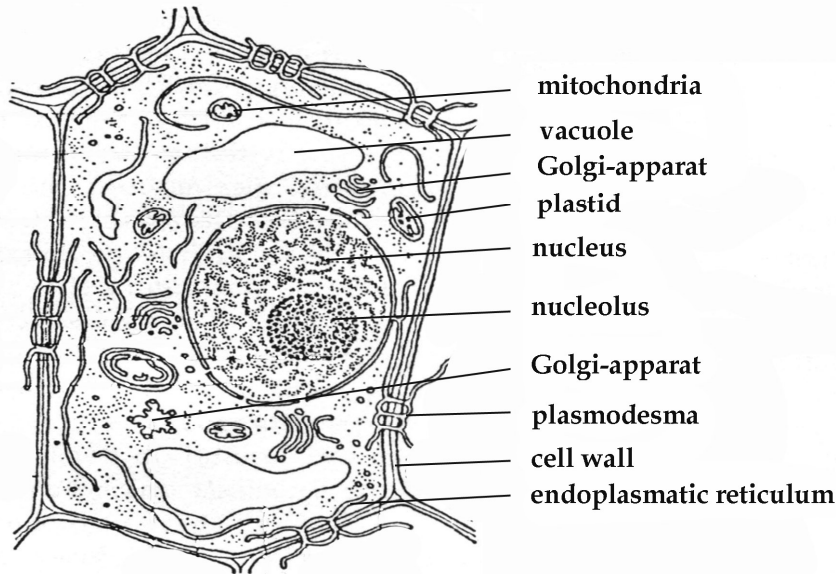


Fig. 2 Eukaryotic plant cell (adjusted according Procházka et al. 1998)

2.1 Membrane complex, semi-autonomy organelles and cytoskeleton

The membrane complex of the protoplast secures **segregation** and **transport** inside and outside the cell and organelle space, allows for the **creation and sustainment of concentration gradients, electric potential and water potential difference**, it **locates synthetic and degradation processes** and **enlarges reaction areas**. The surface of a life cell body is covered with a simple **cytoplasmic membrane** (plasmalemma), which is **semipermeable**, semifluid, made of lipid-proteid mosaic. It is **asymmetric**. It controls transport of nutrition and metabolites, cell wall structure, reception of exogenous signals and connection with the neighbouring cells. The **endoplasmatic reticulum** is a 3-dimensional matrix of simple membranes that make flat containers and tubular creations. It divides the cell space, enlarges the inner area and speeds up the transport of material inside a cell as well as between cells. The synthesis of protein takes place on the endoplasmatic reticulum surface, while the synthesis of lipids and saccharides takes place inside. It takes part in the biogenesis of organelles. Containers of **Golgi apparatus** are attached to the endoplasmatic reticulum (ER). The Golgi apparatus work with the output of ER. The processes of synthesis and transport of cell wall material, secretion activity and creation of vacuoles are carried out there. **Tonoplast** is a similar membrane as cytoplasmic membrane and it divides cytosols from true water dilutions of vacuoles. Vacuoles are primary storage spaces of water, saccharides, amino acids, proteins and lipids; they might be part of lythic (disintegrative) and excretory apparatus and might have protective (bind dangerous ions), defence and alarming functions (toxins, pigments). **Ergastic substances** include starch, lipids, proteins as storage substances, cellulose, lignin as structural substances and substances with physiological and ecological functions (crystalline inclusions, aromatic substances etc.).

The plant cells contain **two types of semi-autonomy organelles (plastids and mitochondria)**; their structure are **similar to simple prokaryotic cells**. In the prehistory they used to be enclosed in eukaryotic plant cells as **endosymbionts**. **Chloroplasts** (centres of photosynthesis) surrounded by a double membrane are a

good example of these. Their interior space is divided by **thylakoids into the grana**, as well as **thylakoids that connect grana (Fig. 3)**. In the chloroplast membranes, there are pigment-protein complexes needed for the reception of radiant energy and its transformation into the energy of chemical bonds of saccharides. **Mitochondria (centres of respiration)** are also surrounded by a double membrane. Their interior surface carries elements of respiration chains and enzymes needed for the formation of ATP (adenosine triphosphate), there is a cycle of acid citric, NAD (nikotinamid adenin dinucleotide) reduction processes and the degradation of fatty acids. What decides on the semi-autonomy of these organelles is their **own spiral DNA molecule** (deoxyribonucleic acid) and the related **proteosynthesis**.

The cell inner structure, organelle position, exterior shape of the cell and its directed growth are guided by the **cytoskeleton** whose specific proteins are organised into **microtubules, microfilaments** and short **microtrabecular fibres**. It carries out transport of cytoplasm using energy (from ATP), controls the position of chloroplasts towards the radiant flow, chromosomes during cell division and it also decides on the place and direction of cellular microfibrils in cell walls.

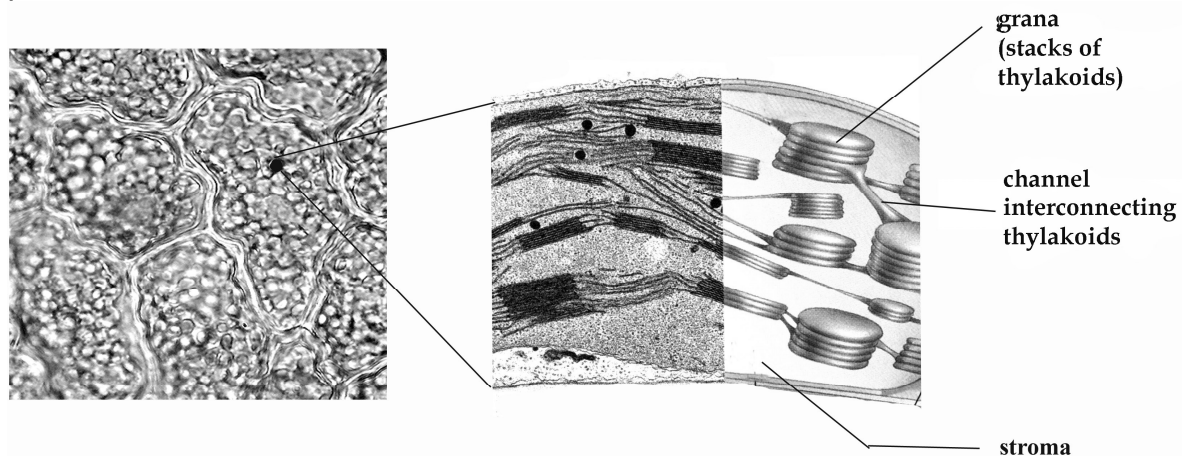


Fig. 3 Chloroplast. Left – oval shape of plastids in the mesophyll cells of spruce needle; middle – picture of inner plastid structure from electron microscope; right – schematic picture of inner plastid structure (adjusted according Solomon 1996)

2.2 Nucleus

Nucleus is the **centre of the interior memory** which is sustained, multiplied and transported into the actual cell and even from generation to generation (of cells as well as organisms). It is separated from the cytoplasm by a **double membrane** with pores interconnected with the endoplasmic reticulum. It **contains a nucleolus, nucleous matrix with ribosomes, nucleoproteins and chromatin**, i.e. nucleic acids that function as a genetic apparatus.

These are **heterobiopolymers** based on the **specific sequence of nucleotides** with purine base (adenine, guanine) or pyrimidine (cytosine, thymine in DNA and cytosine, uracil in RNA). These molecules also contain saccharide pentose (deoxyribose in DNA, ribose in RNA) and a phosphate group. DNA has a shape of a double helix, opposite bases of both the fibres (connected only by a hydrogen bond) are equal (adenine opposite thymine, guanine opposite cytosine). The specification of these acids is given by the sequence of nucleotides, whose **triplets encode a specific amino acid**, and the sequence of triplets is given by the **sequence of amino acids in proteins**. New DNA molecules are always copies of already existing

ones. After the double-helix molecule is unwound and its two fibres are separated, new copies of these fibres are synthesised, so that two new molecules were made from the original one (replication, reduplication).

Proteins are heteropolymers as they are made of the **selection of more than 20 amino acids in various sequence, various number** of repetition of individual passages, **various lengths of the chain** and various possibilities of spacial arrangement. Taking into account all these variations, they have different characteristics (as building blocks and parts of enzymes) and this makes them the primary source of the variability of life forms and originality of each individual. The **synthesis of proteins** proceeds in several stages. In the nucleolus, according to the model – unwound DNA passage, the sequence code of bases is transcript into three types of RNA (mediator, ribosomal and transfer) – i.e. **transcription**. Then these molecules undergo transformations (mutation – cutting out extra passages and making new connections) and then they move from the nucleolus to the cytoplasm. Double-body ribosomes with rRNA (ribosomes aggregation makes polyribosome) join the mRNA fibre, and when moving along the fibre, they match with individual activated amino acids, transferred from the tRNA cytoplasm, according to the triplet sequence – several equal molecules of individual protein are generally synthesised in this way. They originate by the **translation** of information from DNA. These proteins are placed into ER containers, where they are checked and transported into the places of need, or placed into the Golgi apparatus for further syntheses.

2.3 Cell ontogenesis

The **individual cell genesis** (ontogenesis) is divided into the division **meristematic stage** (embryonic), the **elongation stage** and the **differentiation stage** (towards a specific function). **Cell division** (i.e. cytokinesis) is followed by the division of its nucleus – **karyokinesis**. Nucleous DNA condenses, spiralizes and connects with single protein histones to form chromosomes. Nucleus membrane gets dissolved, chromosomes undergo longitudinal division and half of each moves to the daughter nuclei (due to cytoskeleton), i.e. nucleus equational division – **mitosis**. In the newly formed nuclei, transported DNA molecules (chromosomes) are resolved into the functional simple fibre structure and the nucleous structure is renewed. The amount of DNA in daughter cells rises to the original value by means of replication. Cytoplasm as well as all other cell structures, including cell membrane, are multiplied, and the cells prepare for **further replication (meristem cells) or shift towards the next ontogenetic stage**.

Healthy cells (formed by the mitotic cell division) have an **even number (diploid) of chromosomes** (i.e. each chromosome type is represented twice there, i.e. in case of yew tree, the cell nuclei comprise of 4 chromosomes, 12 in spruce, larch and pine, and 26 in maple).

The gametes genesis – male and female sexual cells – is preceded by another karyokinesis type – **meiosis**. It leads to the creation of cell nuclei with a basic set of chromosomes (haploid) which are greatly transformed by the mutual replacement of passages between pairs of mutually corresponding homologue chromosomes. **A new individual initiates from the fusion of a male gamete nucleus** (generative nucleus of pollen with a base chromosome set) **with a female gamete nucleus** (i.e. ovum cell nucleus which also comprises of a base number of chromosomes). This creates **zygote** – the first cell of a new individual – having a double set of chromosomes, one of whose comes from the mother and the other from the father organism . In

angiospermous plants, there is an extra fusion of the second nucleus of pollen (having a basic number of chromosomes) with the central nucleus of the embryo sac which is diploid. This is how a triploid endosperm is made. It feeds the plant embryo until it matures.

The nucleus division, or fusion of nuclei, is followed by the **cell division (cytokinesis)**. Regarding cytoplasm and its structures, **the division is not even**. Some elements reach the daughter cell transformed (e.g. plastids, virus element etc.), so **daughter and mother cells are not equal** (this causes e.g. unevenly coloured stripes or segments of leaves). For instance, it is the prime division of zygote that really decides which of the daughter cells shall become the basis for the above-ground and root structures. Onwards, root cells censure a great deal of information, e.g. that could be used in photosynthesis or blooming. Similarly, mother cells of xylem and phloem are distinct, though they were initiated in the same cambial initial. **In theory, all plant cells include all information needed to create a new plant of a given species** – this allows for the **vegetative reproduction**: a sprout with encoded information on how to build and form shoots develops on a root, or roots may as well be formed on shoot. In general, in the embryonic growth stage, there are intense syntheses of nucleous acids, lipids, proteins. The plant needs a lot of nitrogen and phosphor. The growth regulators of the greatest influence involve cytokines and gibberellins.

The above described stage of the cell division growth is closed by the **construction of a new partition – cell wall**. Its first layer consists of proteins, mainly pectates (salts of pectate acids). It is called **middle lamella** or intercellular matter. After that the new cells concentrate vacuoles, they get filled with water – their pressure from the inside of the cell wall rises and they grow in size (length of cell may increase of up to 20 to 50 times). The construction of an extending wall is finalized by the **primary lamella**. Cellulose macromolecules (homobiopolymers of glucose residues) are inserted into the lamella and get arranged in crystalline microfibrils. Microfibrils may be more or less well structured, interconnected by pectates and hemicellulose (besides glucose they contain e.g. saccharide xylose) with lower proportion of protein. The new matter is inserted by means of intussusceptions – the wall grows in size and does not prevent the volume growth of protoplast. However, bonds between wall parts are weak, cell wall is not solid and behaves as fluid crystal, and this makes the cell susceptible to further changes in shape. After the shape has been stabilized, the ontogenetic stage of the volume growth is closed. What ensues from the description of this stage is that a plant mainly **needs water** as it is the force that extends growing cells and develops a hydraulic pressure on the neighbourhood. Another needed matter **is organically bound carbon (saccharides)** widely used for the formation of cell walls. Regarding growth substances, gibberellins are the ones that are most important at this stage.

As cells enter the **differentiation growth stage**, depending on their future specific function, they build **secondary layered lamellae** to strengthen the cell wall. The lamella is formed by the apposition of further layers from the inside of a cell; i.e. the middle layer is formed first, the primary one follows and the secondary is formed last. The building substances include: cellulose, hemicellulose, lignin, suberin, cutin, waxes, silicon dioxide, carbonates, sporopolenines etc. Since this is a **centripetal growth**, i.e. from the periphery towards the centre (the reverse process, centrifugal growth occurs in cell wall formation of pollen), the protoplast area might be diminished to such an extent that a cell could not survive. In most cases, particularly in skeleton cells or xylem conductive cells (with variable pressure conditions from

overpressure to underpressure as low as 3-4 MPa) the **secondary lamella is formed unevenly**. Precise direction and laying construction is driven by cytoskeleton and complex structures is form. **Pits**, e.g. simple or branched ones, mediate connection and communication through plasmodesmata (cell wall channels lined with cytoplasmic membrane that connect the protoplasts of adjacent cells) among cells as well as organs (by means of long and medium distance diffusion), which helps sustain balance in an individual. Bordered pits (in gymnospermous tracheid walls) and even **perforations** (e.g. in vessels, laticifer ducts) enable material flow on long distances. Various types of **thickening** (round, spiral, step, matrix) **prevent from cell deformations** (e.g. phloem and xylem fibres, sklereid etc.). Construction and material structure of cell walls reflect their basic characteristics; i.e. insolubility in water, anisotropy (e.g. birefringence in polarized light and spacial distinct changes in volume during growth) but also the ability to **communicate with the neighbouring cells or water and gas permeability**. There are numerous instances when the **cell wall features are not compatible with protoplast existence**, so after the wall is formed, **protoplast dies** out and its functions (mainly mechanic, conductive) are taken over by the cell wall.

There are two types of factors on the differentiation stage of cell life: **endogenous** – i.e. genetic, enzymatic, phytohormonal activities, and **exogenous** – e.g. climatic, soil, topographic (relief and morphology) and biotic (e.g. galls on leaves brought about by fault cell differentiation as an impact of insect activity). There is an increase in the consumption of mineral sources and the demand on the optimal photosynthesis and respiration. Some kinds of already specialized cells are capable of **dedifferentiation**, i.e. return to the embryonic stage and could restart division. This is why **surface injuries** may **regenerate and heal**.

3 Tissues

Woody species have **true tissues** (originated from a single cell) and are defined as groups of **cells of the same shape and functions**. They share some common features. For instance, the cell walls are interconnected by intracellular material (middle lamellae comprised of calcium magnesium pectates). **Life cell** (protoplasts) are **interconnected by plasmodesmata** with the tubular endoplasmatic reticulum. By means of these, all life cells of the **whole system form one unit – a symplast**. It can actively transport (by speeded up diffusion) substances that have been formed or transported through cytoplasmatic membranes in another part of a plant.

Another feature of tissues is the **presence of intracellular spaces**. They are formed in three different ways:

- **schizogenous** – by splitting of middle lamellae (e.g. in corners of cells or between guard cells of epidermis) or by tissue injury when intracellular material and walls may be dissolved (**Fig. 4**)
- **rhexigenous** – by tearing off tissues due to fast growth of neighbouring tissues (e.g. in pith, especially in monocotyledonous liane stems)
- **lyzigenous** – by dissolving of cells (essence reservoirs isolated by lignified or corked walls of neighbouring cells)

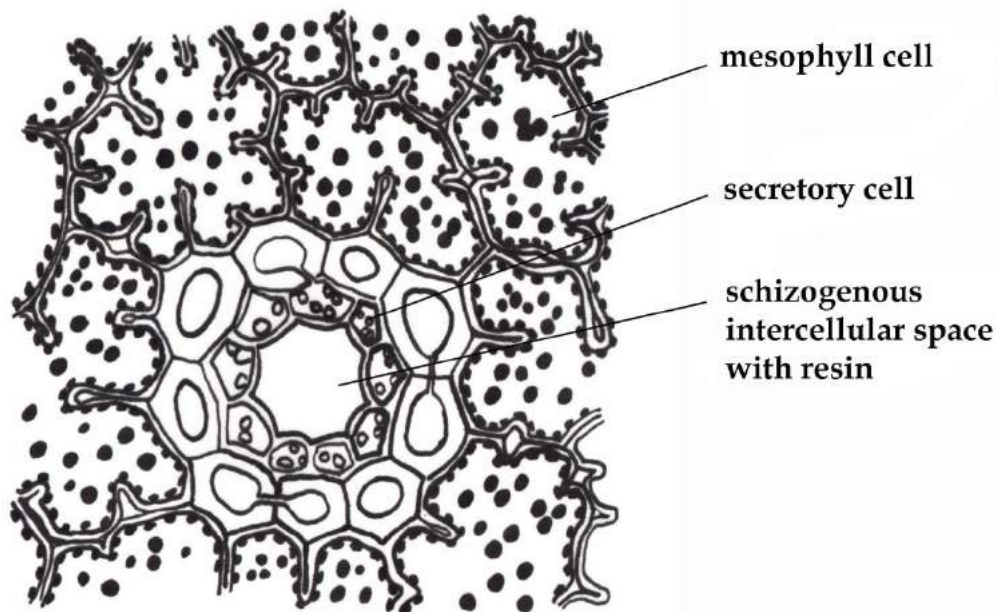


Fig. 4 Schizogenous intercellular space – Resin duct in the pine needle developed by splitting of middle lamellae of secretory cells.

Intercellulars hold a substantial role in **transport of gases and water** (e.g. in leaf spongy parenchyma, leaf hydathodes and lenticel filling tissue) and in **concentration and isolation of protective substances** (e.g. resin canals and silicae containers). Schizogenous intercellulars with aeration functions grow at decreased aeration in inner tissues (in roots during soil flooding, in stems and branches lay on the ground etc.) They give such a tissue its name – **aerenchyma**.

Intercellular areas (except for excretion glandule, resin and laticifer ducts) as well as interior areas of dead xylem cells (e.g. vascular bundles) **create an apoplastic matrix** – a **communication system** which transfers matters in gaseous, liquid and solid phases **without crossing barriers of cell membranes**. Even saproparasite organisms could spread through the apoplast.

Idioblasts are commonly present in tissues – these are cells that **considerably differ from the majority of cells by the shape, type of the cell wall** (e.g. sclerid) or by the contents (crystals, tannin in vacuole, e.g. tannin cells near phloem in spruce etc.)

Tissues are categorised by various criteria. From the perspective of a **cell wall type**, cell lifespan and function these tissues are distinguished (**Fig. 5**):

- **parenchyma** – thin-walled cells, mainly living, capable of division, metabolic, storage etc. functions
- **collenchyma** – living cells with unevenly thickened cell walls. If they thicken at cell corners this is called angular collenchyma, if thickened walls are parallel to the organ surface, this is called tangential collenchyma, if it contains intercellulars, it is known as lacunar collenchyma); it acts as a mechanical support, metabolic support, it can renew division and give rise to healing tissue
- **sclerenchyma** – tissues that contain mainly dead cells whose function is taken over by strong lignified walls. The walls are filled with various types of narrowings as well as thickenings – round or spiral ones that do not slow down the elongation growth of neighbouring cells or matrix and staircase thickening that occur in the parts of a plant where the elongation growth is no more as active as it used to

be. Sclerenchyma cells have mechanical (supporting) and transportation functions. They transport solution from roots to the above ground parts.

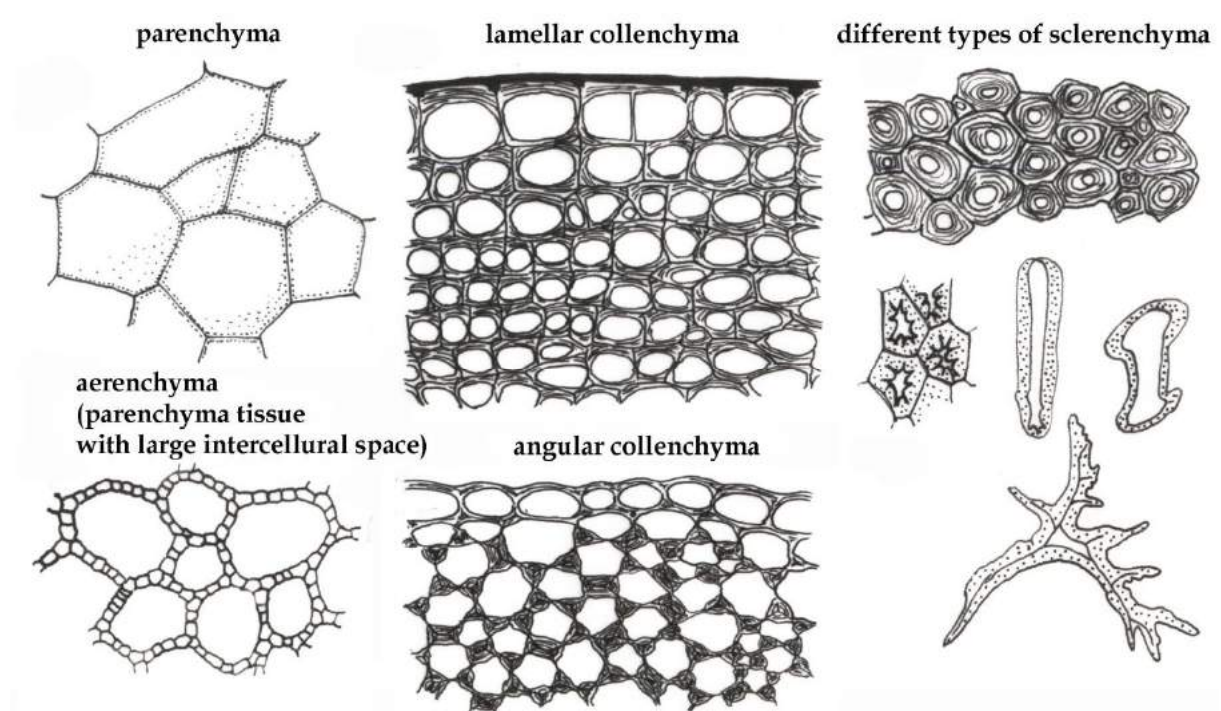


Fig. 5 Tissues division from the perspective of a cell wall type and cell lifespan: parenchyma, collenchyma and sclerenchyma

There are **two types of cell from the perspective of cell shape** – **isodiametric** (i.e. star-shaped, spongy, palisade etc.) and **prosenchymatic** (highly elongated cells). From the perspective of the **rate of differentiation**, the following types are defined: **meristem** – dividing, embryonic, which never reaches growth and differentiation stages, localized in growth zones as apical **primary meristems** (on stem, bud and root tips, or on a growing section of a leaf) and **lateral secondary meristems**. By cell differentiating, meristem gives rise to **permanent tissues**, also divided into **primary and secondary** ones. They are functionally arranged into the systems of **covering, vascular and basic tissues**.

3.1 The origin of primary meristem

The whole **tree organism** originates in a **single cell** called **zygote**. It is the initial cell of an offspring organism which was formed by the fusion of a sperm cell (male) and an ovum (female) cell, called gamete.

Zygote is **bipolar**, i.e. there already exists a physiological difference which later, when organs and whole organisms are formed, **directs the flow of material, photosynthates, hormones** and other controlling substances. This polarity also directs the formation of **adventitious roots and buds** from stem and root. In case of stem, new roots are formed at basal (proximal) cutting area and new buds at apical (distal) poles; it is opposite in root sections.

The zygote polarity defines the **basic features of root and above ground systems** as early as the first cell division. The onward cell dividing with genetic regulation leads to the creation of an embryo of a plant. **Embryo contains all merismatic**

cells, i.e. cells capable of intense dividing. A mature embryo contains: a **radicula** – later develops into the primary root; a **hypocotyl** – primary part below cotyledons, stem part bearing primary leaves – **cotyledons** (monocotyledonous plants have one, dicotyledonous have two, gymnospermous have multiple cotyledons). In the tray of cotyledons, there are primordia of the first lateral buds and **epicotyls** between cotyledons – a primary above cotyledon part of stem enclosed by a **plumula**, i.e. apical shoot of the above ground system (**Fig. 6**).

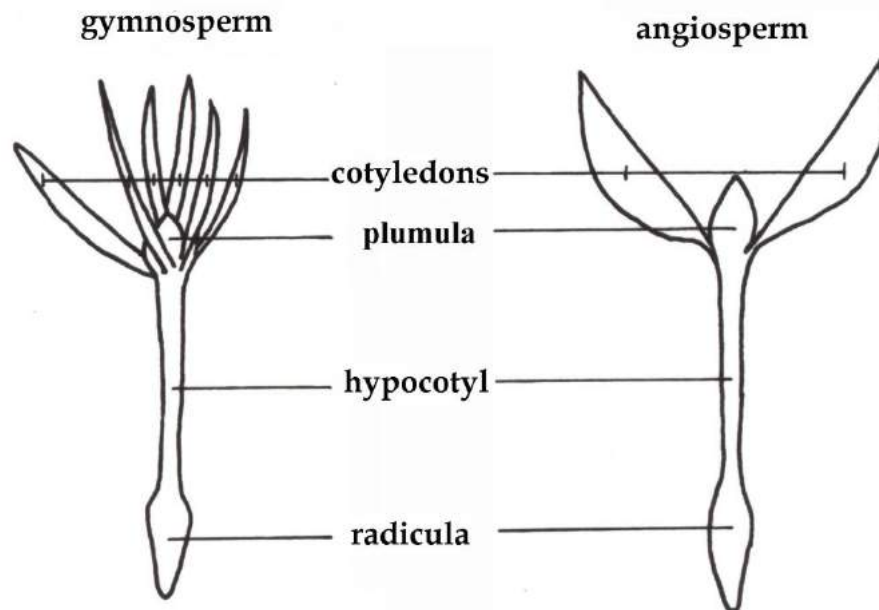


Fig. 6 Schematic picture of germinate plant. Left – gymnosperm; right – angiosperm

3.2 Primary meristems

All cells of a plant divide during the **germination and growth**, but they **gradually lose dividing capability**. They start growing towards the base (in proximal direction) and focus on special functions in dependence on their positions. This means that meristems move in distal directions, i.e. above-ground grows towards the sunlight and to the root apex (grow in direction of gravity).

Dividing character is retained only in the **apical cell groups – initials**, that occur at the main root apex, later in lateral roots and on the stem apex and lateral shoots (**Fig. 7 and 8**). The initials are directly **connected to the embryo cells** (archimeristems); and together with the newly divided or just being divided derivatives they form a **protomeristem**. Its older derivatives still capable of dividing form a **protoderm** (giving rise to the primary epidermis tissues), **procambium** (whose dividing cells arranged in stripes differentiate into primary vascular tissues – xylem, and phloem) and the **basic meristem** (predecessor of epidermis, pith, pith rays in stems and roots, mesophyll in leaves).

Protomeristem, protoderm, procambium and basic meristem are **primary apical meristems** responsible for the **elongation growth** and for the formation of a **set of primary permanent tissues**; their spacial arrangement decides on the primary structure of organs. The meristems may retain in the **latent state (suppressed buds)** for a long time. They generate leaves and buds in their trays as basics of lateral branches. Suppressed buds are a storage which can easily regenerate a plant. On the other hand, they can lead to the formation of various tumours by

pathogens. Between stem nodes with leaves from the primary meristems, there is an **intercalary meristem** which allows for later elongation of internodes. **The shape of leaves** ensues from different activity of the residue meristems on the basis, tip and edge of their blades.

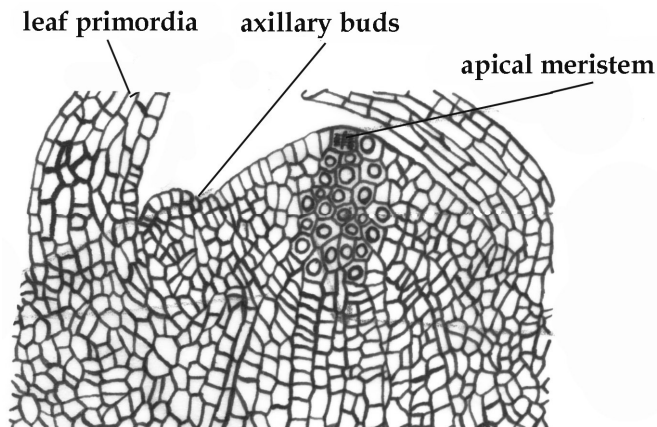


Fig. 7 Primary meristems of shoot apex. Leaf primordia protect apical meristem. Axillary buds are form in the leaf primordia base.

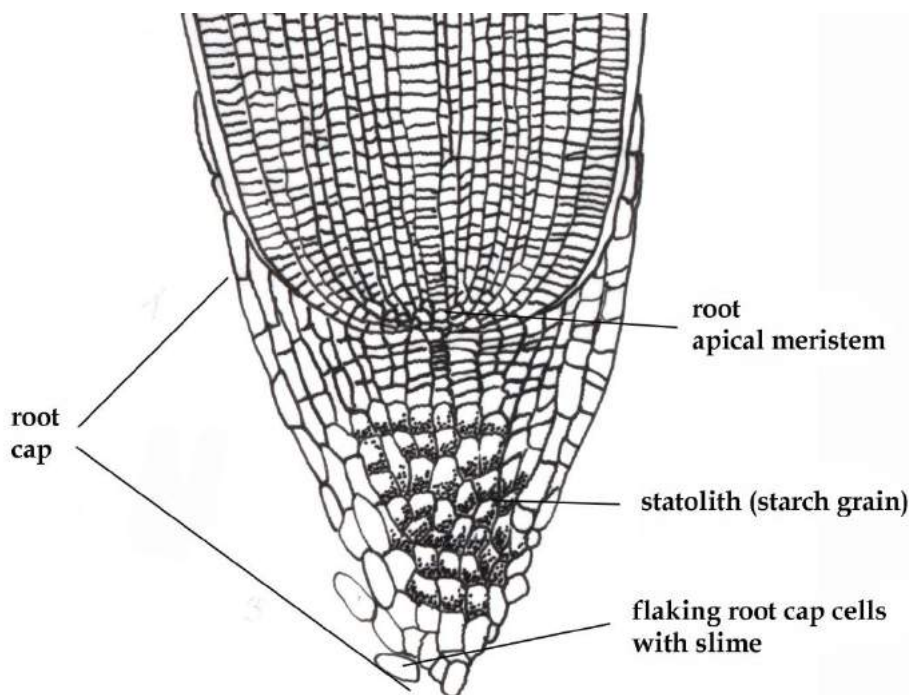


Fig. 8 Primary meristem of root apex. Root cap protect root apical meristem and enable root growth in the soil. Lateral root are form later.

The **primary structure** of stems and roots is typical to some **herbs** (e.g. in *Ranunculaceae* family) and **monocotyledonous woods** that do not secondarily grow in diameter. **The structure of the other woods that form secondary meristems is more complicated.** Its appearance can be well described by means of **three mutually perpendicular sections**. The **cross-section** is perpendicular to the longitudinal axis of an organ. The **radial** section is longitudinal and crosses the

centre of an organ. The **tangential** section is longitudinal too, but it does not reach the centre, it remains at the periphery.

3.3. Permanent primary tissues

3.3.1 A system of primary surface tissues

The differentiation of protoderm derivatives in **above ground organs** leads to the formation of compact, unwettable **epidermis** covered with **cuticle and epicuticle wax** from the outside. If epidermis is multilevel, then the inner layer is called **hypodermis**. It is gas proof except for **stomata**, it protects the inner tissues from UV radiation which effectively absorb, and it serves as a water reservoir. By means of opening and closing stomata, it **protects a plant** from withering, overheating by transpiration (distribution of water gas to air) and from biotic factors. **Trichomes** (outgrowths of epidermis cells) are helping to fulfil epidermis functions. These trichomes might be single-cellular or multicellular (**Fig. 9**), branched or unbranched, glandular. More massive formations are called **emergencies** which consist not only of epidermis but also inner tissues (**Fig. 10**). These involve: **prickles** (rose, raspberry), **glandules** (in ash tree or chestnut shoots), or **pollen section** in flowers.

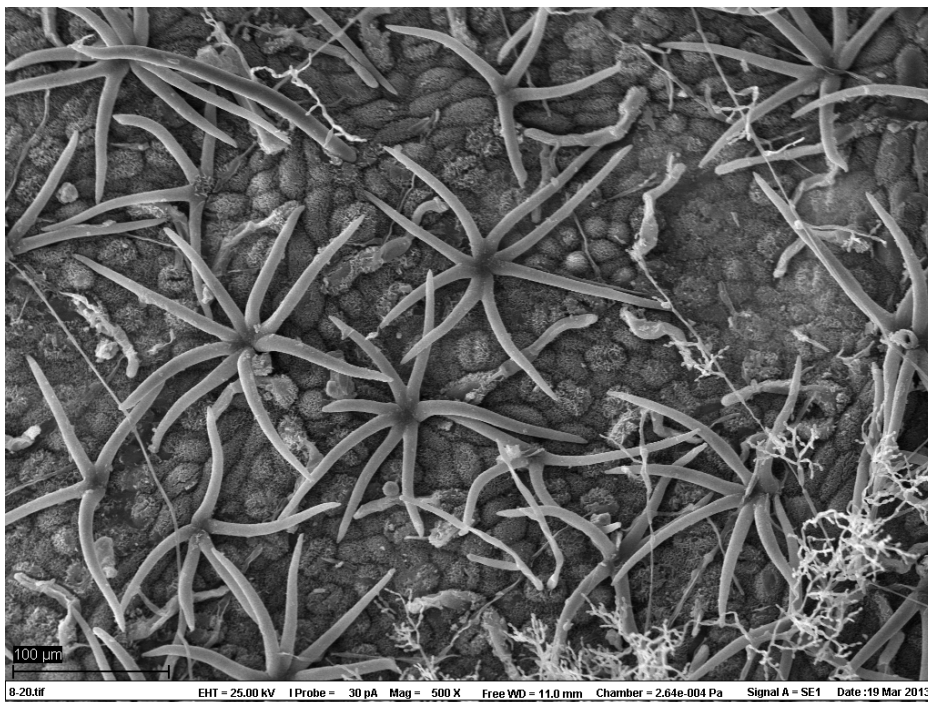


Fig. 9 Multicellular trichomes of *Viburnum rhytidophyllum*



Fig. 10 Prickles (emergencies) of rose. They consist not only of epidermis but also inner tissues. Unlike spines they are form irregularly.

In case of **roots**, **rhisodermis** is formed. It has weak cell walls, it is **less water and gas resistant**, it **swell when wet**, it has **no cuticles** or stomata. The rhizodermis produces acids and exoenzymes that disturb the substrate and nutrients. Vacuoles contain **osmosis active solutions**, cells lack chloroplasts, stomata, cutin and wax, but they have leucoplasts. There are **rhizomes**, parallel to trichomes, but unlike those, they have the absorption function. They are shorter and less condensed in trees than in herbs, they are lacking in case of root colonisation by mycorrhizal fungi. Taking into view the characteristics of rhizodermis, roots are very sensitive to drying out. Fine roots of seed plants removed from the soil, left in the sunshine and on dry air may die in a couple of minutes.

3.3.2 A system of primary basic tissues

Primary cork called cortex is a basic multicellular **tissue between the epidermis and vascular tissues**. In roots, outer layer (**exodermis**) cells have protective functions (corked later replaced the rhizodermis), medium layer (**mesoderm**) have transportation and storage functions. **Endodermis**, inner layer is made by cells with widened, corked stripe of cell wall (i.e. **Casparian strip**) and **cells above vascular tissue that are permeable** – this is a means of endodermis control intake of substances into vascular tissues in the central cylinder. **Primary cork of shoots** has a **photosynthesis** function, **storage** function (life parenchyma cells) and a **mechanical** function (collenchyma and sclerenchyma). Life primary cork cells are capable of meristematic activity after an injury.

The primary cork is linked to the central stem and roots parts by the **pith rays**. They secure **horizontal transport** of substances, e.g. oxygen from the atmosphere and saccharides from xylem to dividing and growing cells in the cambial zone. Pith ray cells are a reservoir of crystals, phenolic and toxic substances; there are horizontal resin canals in many gymnospermous plants. **Pith** occurs inside stems, hardly ever inside roots. Its thin walled cells in young stems may contain chloroplasts or starch, later on secretions and lignin in cell walls.

Basic tissues involve **mesophyll** in leaves – a tissue with photosynthetic functions. It is the most significant producer – **source of saccharides**, molecules rich in energy adenosintriphosphate (ATP). These are formed using solar energy for the chemical transformation of atmospheric carbon dioxide and water.

Basic tissues have a lot of functions: assimilation, reservoir, mechanical (collenchyma, sclerenchyma) and **excretive** (hydroids, nectarines, resin ducts etc.).

3.3.3 A system of vascular tissues

It is a **vascular bundle** that **interconnect distant parts of a plant** by means of distributing mineral substances, saccharides, regulation molecules. **Vascular bundles may be complete** (containing both xylem and phloem parts), or one of these parts may be absent (**incomplete vascular bundles**, e.g. apical parts of tree tops or foliage mesophyll). Their **primary structure is retained in monocotyledonous** woods and woody **ferns** and their **arrangement is scattered** and vascular bundles are either **concentric** (phloem-centric, phloem is surrounded by xylem, e.g. *Pteridophytes*) or **enclosed collateral** (centripetal xylem and centrifugal phloem – palm trees). Such vascular bundles could be divided in two subgroups at the final stage of the development – **older protoxylem** (thinner vessels, cell walls are reinforced by circle or spiral thickening) and **protophloem** with obliterate or dilatate (i.e. non-functional) cells. The latter is younger – with fully developed and more efficient **younger metaxylem** with broad tracheids or vessels and **metaphloem** with functional sieve tube and sieve cells. The mentioned **vascular bundles are created** by general and complete differentiation of **procambium** strips.

Vascular bundles in stems of gymnospermous and dicotyledonous woody plants are **collateral, open** (i.e. procambium stripes are only partially differentiated, so **cambium** between the phloem and xylem remains active), **arranged in circle**, separated by rays. Protoxylem lies on the periphery of pith and metaxylem is located centrifugally. As early as the first year of stem development, the metaxylem neighbours with the **secondary xylem** (deuteroxylem) in stems and roots. The passage is gradual, it may even be less perceptible. On the edge of the central cylinder, there is protophloem which is no more functional, centripetal metaphloem and towards cambium there is completed **secondary phloem** (deuterophloem).

In early stages of development, **roots have radial vessel system**, whose individual incomplete vascular bundles rays where **xylem and phloem groups are alternating**. Vessels in monocotyledonous roots are organized in multiple groups. Gymnospermous and dicotyledonous plants have usually monarch (one group of xylem and phloem), diarch (two groups of xylem and floem), triarch (three groups of xylem and phloem) fine roots. Cambium in gymnospermous and dicotyledonous roots start to form below the phloem groups and above xylem groups later on. The radial vessel bundle passes into multiple open collateral vessel bundles arranged in a circle and separated by phloem-xylem rays.

3.4 Secondary meristems

3.4.1 Cambium

Primary structure in woody plants is retained only for a short time. Procambium is active and changes into the **secondary lateral meristem – cambium**. Below the outer layers of tissues (epidermis, primary cork, primary phloem), cambial initials

form a coherent cover of a cylinder that appears as a **cambial circle** on the cross section. It contains sections of **fascicular cambium** responsible for **extending of vessel bundles**, and sections of **interfascicular cambium** giving rise to **phloem-xylem rays**. Bundle cambial initials are longitudinal in direction of a long axis of an organ and separate mother cells of the **secondary xylem** centripetally, and mother cells of the **secondary phloem** in the opposite direction. Transverse partitions between daughter cells are parallel with the surface of organs (**periclinal**). When daughter cells arranged in radial lines grow, the whole organs grow with them. As early as the first year of activity, some initials of cambium go under such a division that cell walls separating daughter cells are perpendicular to the surface of the organ (**anticlinal**). It results in the creation of **new initials of interbundle cambium**, i.e. in the **rise in diameter of the cambial circle** and rise in number of vessel bundles and rays. In that case, rays do not reach as far as the pith or primary cork. Such rays are called **secondary phloem-xylem rays**.

Intrabundle cambial initials are nearly isodiametric (same size in all directions). They divide ray cells of the same type in both directions – centripetally as well as centrifugally. Cambium is responsible for diameter growth of the stem and root systems. However, while it creates one annual ring (early and late wood) in the stem system during a growing season, and the number of annual rings more or less corresponds to the age of a tree part, in case of roots, it is different. There are more growth waves in a year. These are irregular and their boundaries are less obvious, so it is not that easy to determine their age. In evergreens, cambium appears in leaves, too (in veins of the first or second order) and there are more phloem than xylem layers in needles.

Phloem is conductive tissues that transport carbohydrates from the locations of syntheses to the consumption locations: meristems, root systems, flowers, fruit or buds). In **gymnosperms** phloem tissue is made of **short-life sieve cells** with dense **sieve areas** located mainly in cell walls with connection to albuminous cells, which neighbour with pith rays. In **angiospermous** species, this tissue is formed by **elements of sieve tubes (Fig. 11)**. The tubes are made of cells arranged in vertical lines. These are longer conductive passages. Sieve tube elements are elongated in direction of a long axis of an organ and they dissolve cell nuclei during the process of differentiation. This means that they lose the information bank, cannot react to changes that may occur and their lifetime is extremely shortened. Longitudinal cell walls are perforated into the **sieve area** similar to sieve cells, but there are large **sieve pores** on the connection of two sieve tubes. Cytoplasmic membrane passes from one element to another and distributes organic material (esp. carbohydrates) into all places of consumption in a plant body.

The content of sieve tubes demonstrates positive pressure (approx. 3 MPa) on the inner walls, carbohydrate solutions may be concentrated even more than 20 % and the speed of transport is approx. $1 \text{ m} \cdot \text{h}^{-1}$. The sieve pores are plugged by polysaccharides **callosa** originated from glucose remains, which is produced and stored at the end of the growing season. This process **close conductive pathways in sieves** sooner than usual. Sieve tubes may be accompanied by phloem parenchyma (**soft phloem**) and sclerenchyma fibres (**hard phloem**). Non-strengthened walls of older sieve tubes allow for the obliteration by the pressure of the surrounding tissues. The pathways are hardly ever active for more than one growing season (e.g. in lime or *Tsuga canadensis* – hemlock). The **secondary phloem** is formed by cells divided by cambial initials within open vessel bundles of gymnospermous and dicotyledonous woods. It is renewed each year. In

monocotyledonous woods, e.g. phloem-centred draceana, it can also stay active without a renewal.

In autumn after the finished elongation and diameter growth of stem in wood parts of vessel bundles, we could observe **protoxylem cells** located between typical wood and pith – they are tiny, thickwalled. Out of the protoxylem, xylem cells are larger in diameter (**metaxylem**) and finally, **secondary xylem cells** are observed (firstly early wood and then late wood). Small cells from the previous growing season are covered with a new layer of early wood of large diameter cells and thinner cell walls. This makes the **annual ring** border well observable.

If the growth is not interrupted (esp. in young trees), the **number of annual rings** on a stem base tell us the **tree age**. Based on the appearance and arrangement of early and late wood cells, deciduous trees are categorized into **ring porose, semi-ring porose and diffuse porose** ones. A ring of extremely thick vessels which quickly pass into a number of radial lines of thinner vessels and other wood elements with smaller diameters (e.g. ash tree, acacia) is formed in spring in trees with ring pores arrangement. Regarding semi-ring and diffuse porose ones, the inner diameter of vessels is diminished gradually and the boundaries of annual rings may not be well observable. The cambial ring grows in diameter as the number of initials multiplies. The number of vessel bundles and rays slowly grows. The **rays** that were formed at the plant origin, stretching from the pith to the primary cork, are called **primary**, and the ones that were formed later, are known as **secondary or phloem-xylem rays**. These are shorter in the radial direction.

According to xylem type we distinguish between **homoxyllic** (gymnospermous) and **heteroxyllic** woods (angiospermous). Wood structure in **homoxyllic** is simpler as there is no division between conductive and specialized cells with mechanical functions. Both **conductive and mechanical functions are controlled by tracheids**; elongated, prosenchyma cells without cell wall perforations. Water dilutions pass from a lower tracheid to an above one through border pits on the radial walls. Parenchyma is mainly found in rays of various width and height. **Annual ring boundaries**, specifically latewood with thick lignified tracheids of little diameter, **build a barrier from freeze, fungi or insects damage**. The essential protective system is a three dimensional net of resin canals, located in wood vertically, and in pith rays horizontally. The **heteroxyllic** species (angiospermous, e.g. deciduous trees) contain special **conductive cells – vessels**, but tracheids are also present.

Vessels are columns of dead tubular cells with perforated transverse cell walls and longitudinal walls with pits and thickenings (**Fig. 11**). In case of ring porose species, early vessels have large diameter (up to 0.5 mm) and high sap flow (over $60 \text{ m} \cdot \text{h}^{-1}$ in lianas). They are often found under a great negative pressure, which occurs when the evaporation from leaves is faster than the root uptake of water from the soil. In this case, they are sensitive to functional disorders due to the penetration of air (**air seeding**) into the vessel (embolism) or penetration of xylem parenchyma from the neighbourhood. Parenchyma spreads in the vessels interior, fills the vessel in and gives rise to **thyloses**. Xylem fibres (**libriform fibres**) are responsible for the mechanical resistance of wood. They are thin, long, usually dead cells with thick lignified walls. It is mainly **parenchyma** that is responsible for the storage function. There are two type of parenchyma - axial, parallel to the longitudinal axis of an organ and usually accompanying vessels and horizontal, i.e. parenchyma of pith rays.

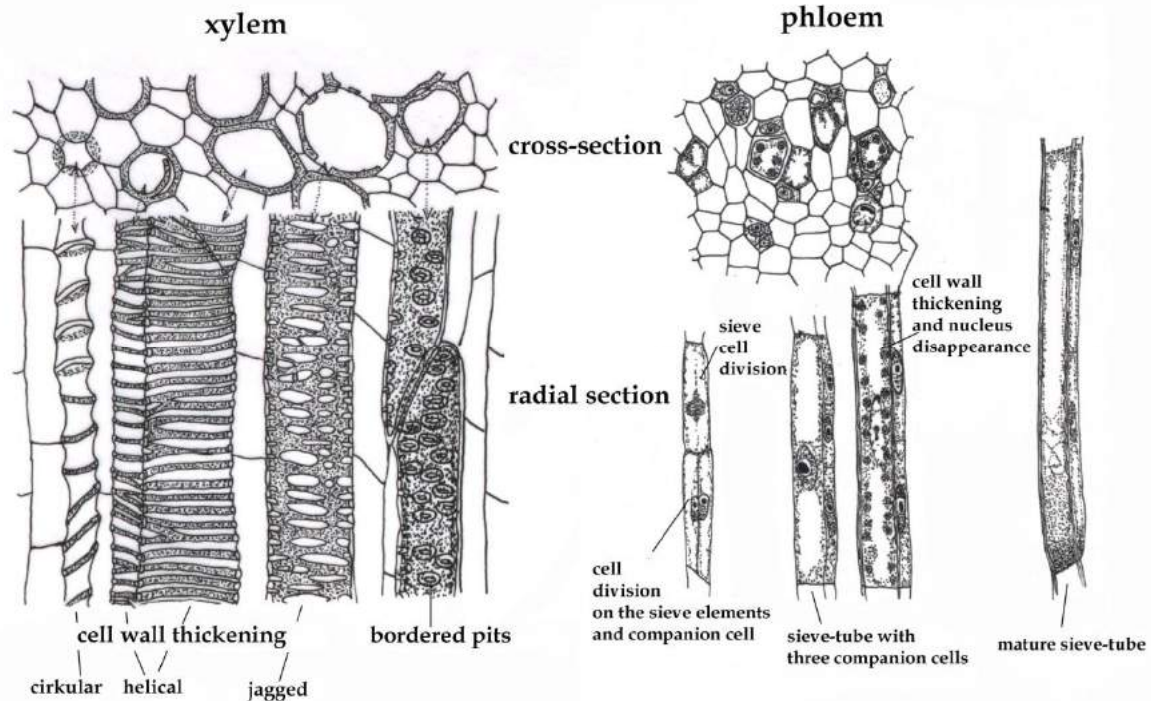


Fig. 11 Vascular bundle is composed of xylem (left) and phloem (right). Both parts are shown on the cross and radial section. Sieve tube development is shown.

3.4.2 Phellogen

Together with the cambium activity and every new growth of xylem, phloem and parenchyma of rays, the plant diameter **extend and develop a pressure** on the outer layers of cells in the radial direction. This results in the formation of another lateral secondary meristem – **phellogen**, which might be located below epidermis, in primary cork or in pericycle in gymnospermous species.

Double-sided dividing of daughter cells is typical of the phellogen. The inner daughter cells live longer and form so called **phellogen**. The outer daughter cells store suberin in the cell walls; and as they become cork, water and gas resistant, they gradually die. They function as a dead tissue – **cork (phellem)** that protects the inner parts of a tree from the exterior danger. The layer of **phellem, phellogen and phellogen** is considered a **secondary cork**.

Though, such a system of surface tissues is not permeable. Other elements must be formed to let oxygen pass to life meristem cells (cambium, phellogen) and life phloem, xylem and ray parenchyma cells in the secondary cork (or even closer). These elements are called **lenticels (Fig. 12)**. They are tiny, they have a rounded or line shaped cracks in the bark of trunks or branches, or in the epidermis of green stems (e.g. spindle tree) or epidermis of fruits. They originate by quick dividing of parenchyma cells by the phellogen cells towards the outer parts of stems. The tissues with rich intracellular spaces aerate neighbouring deeper tissues. The lenticels are frequently formed above xylem rays. In pre winter period, the **lenticels get covered** with water and gas resistant cork cells, thus a protective closing layer is made. This layer only lasts till spring when it gets torn by the pressure of the newly produced cells.

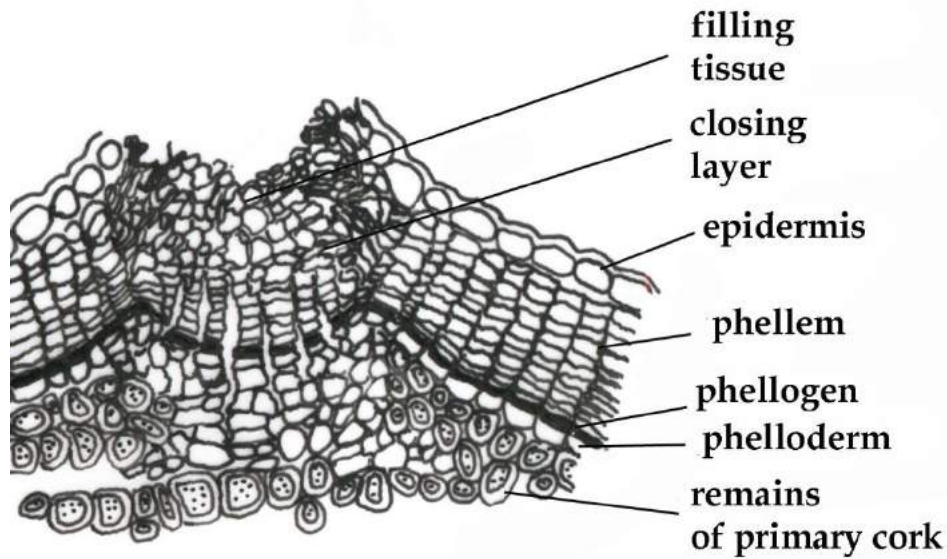
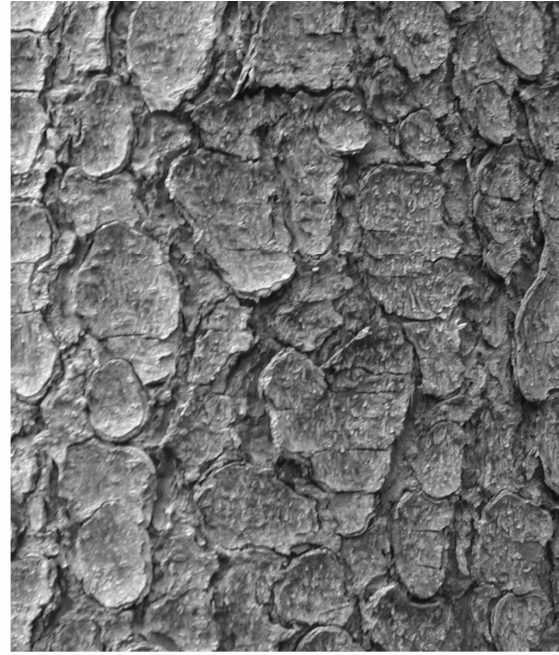


Fig. 12 Lenticel – cross-section of *Sambucus nigra* shoot. Faster production of phellem resulted in epidermis rupture and lenticel formation.

The activity and **lifetime of phellogen greatly varies** from species to species. In some species (beech, hornbeam), phellogen cells are able to **grow in number by means of anticline** division. The phellogen ring growth is influenced by trunk thickening, which is carried out by the activity of cambium. Bark of such trees is smooth. In other instances, phellogen cells are not able to form anticlines and divide only by means of periclinal. The phellogen gets crack and gradually **dies out** as a result of an increasing radial pressure by newly developed annual rings. In deeper primary cork tissues, later on even in life phloem, **new phellogen** is formed. They give rise to new layers of periderm under dead outer layers. The **repetition of dying and the formation of new phellogen** is a unique complex where **dead layers of primary cork meet layers of periderm, and, later on, dead layers of phloem meet deeper and deeper formed periderm**. This tertiary complex of cover tissues is called **rhytidome or bark**. When it is peeled off, the older non-functional layers of phloem are peeled, too. This could be macroscopically observed as a coarse, deeply cracked bark, which varies according to species (trunk base of old pines, birches etc.). The following phellogens could occur in **concentrated rings** – in such a case the bark is known as **ring bark** and peels in longitudinal or cross stripes (juniper, cherry), or the new phellogen is formed deeper and **deeper as smaller or bigger lamellas**, and bark peels off as large scales (plane trees) or small scales (spruce) (**Fig. 13**).



A



B

Fig. 13 According to the activity and lifetime of phellogen great variability of bark are formed. A – ring bark (*Juniperus* sp.); B – scale bark (*Picea abies*)

Another latent meristem is called **pericycle**. It occurs at the edge of the central cylinder and together with cambium it may participate in the formation and growing of lateral roots or formation of adventitious buds or roots, but it can also sclerify and make a heavy mechanical support of phloem (*Aristolochia durior*).

4 Roots

4.1 The origin of root

The oldest vascular plants used to be rootless. Even these days, all vascular spore-bearing plants only have lateral roots of the adventitious origin. **Typical roots** can be only found in **seed plants**. They are developed already in the embryo stage (radicula).

In **gymnospermous** and **dicotyledonous** plants **root growth** (during germination) is **direct continuation of radicula**. Such a root is called **primary**. Majority of lateral roots on this primary root are formed as late as the post-embryonic stage. The outcome is the formation of the **allorhizic root system**, which is divided in the **primary root** and **lateral roots**. Later on, new roots may grow on old roots, trunks or branches (leaves). They are called **adventitious roots**. In **monocotyledonous** plants, there is a **homorhizic root system**. A large number of **lateral roots** are found even in the embryonic stage and **radicula dies** out in early stages of a plant growth. A couple of solid roots are based on hypocotyl. Moreover, the root system is further extended by branching as well as establishing further roots on hypocotyl and higher positioned stem nodes.

4.1.1 General characteristics of root systems in trees

Root is prevailingly an **belowground** organ, which is **heterotrophic** and **non-segmental**. Along with the development of the above ground system, the root system grows by means of branching of the primary root. Roots have a **radial symmetry** and are **bipolar**:

- the first pole – **root apex**, is **distal**, i.e. distant from the mother root or stem
- the second pole – **root base**, **proximal**, i.e. is connected with the mother root and with the stem base).

This polarity is retained even at injured roots and regenerating root sections: roots (more numerous and finer) are formed at the distal area and formation of adventitious shoot buds at proximal area. **Root functions depend** on photosynthates (esp. on carbohydrates) derive from the above ground photosynthesising organs (leaves, i.e. from **primary sources**), or from cotyledons or endosperm (i.e. from **secondary sources**).

Endogenous and **irregular branching** gives origin to the multilevel root system. Root branches are called lateral roots of the primary, secondary etc. orders. They are formed in an **acropetal order**, in other words, the youngest branches are always nearest to the apex tip. This type of branching is called **monopodial (Fig. 14)**. **Sympodial** branching (lateral branches are more dominant than the primary root) is less common. This branching pattern can be found in some trees with mykorrhizza (*Pinus*).



Fig 14 Fine roots on Norway spruce growing in the aerated and nutrient rich soil layer. Root branching is monopodial, regular and rich with many active root tips.



Fig. 15 Fine root of Norway spruce growing in the heavy and wet soil in the 1 m depth. Root branching is irregular, mostly root are dying, lateral root are short with spare root tips.

Lateral branching of roots usually occurs in an endogenous way. The lateral roots are formed inside the branching root from the latent meristem, **pericycle**. Cytoplasm is accumulated at some places in pericycle cells and the cells begin to divide both in the radial and tangential directions. The base of a lateral root is established. Further on, the root penetrates the primary cork and rhizodermis to get to the surface. The origin of lateral roots is not accidental. If the branching pattern is observed in detail, it is clear that they are arranged in **longitudinal lines**, i.e. orthostichies. Cross sections demonstrate that the position of lateral roots is related to the position of xylem and phloem section of the vascular bundle. In some species, lateral roots originate in longitudinal lines opposite to the phloem parts, but most common occurrence is between the phloem and xylem. **Root shortening** (removing the root apical tips) **launches the branching**. In practice, this is applied in pricking off, replanting small plants or cutting of seedling roots, used to support **rich growth of the root system**.

As well as the above ground system, the **root system grows for the whole lifetime without limitations**. Roots grow in length (primary growth) and in diameter (secondary growth). In case of an adult plant the size of the root system remains more or less unchanged. The ratio of dying off old roots equals the ratio of formation of the new ones; the turnover **is balanced**. It is similar to what happens in the above ground structures – treetop volume and the total area of foliage remains unchanged. **The lifetime is influenced** by factors such as type of roots (anchor – long life, elongated – long life, fine – short life), wood species and other conditions, both endogenous and exogenous. **Types of root systems** of trees as widely described in literary sources are generalised and regard individual species that live in the optimal soil conditions. These root system types include **superficial** (plate) root system, **tap** root system, **heart-shaped** root system. Yet, the **variability of the root** systems is much higher than the changeability of treetops which corresponds to the fact that the soil conditions are more heterogeneous and the shape or root systems change during ontogenesis. For instance, a superficial root system may be observed in pine (*Pinus sylvestris*) or beech (*Fagus sylvatica*) if they occur in swampy soil. Moreover, it is frequent that the roots develop asymmetrically. Reaching of roots into the **depth of up to 2 meters** may be even found in compacted and unsuitable belowground

conditions in case of young trees. **Adult and old trees** need to decrease consumption of energy so they limit the diameter growth, lower treetops and **gradually move the root structure up** into the higher surface horizons.

Root biomass makes up of about a third to a half of the biomass of the whole tree, depending on site. The poorer the soil is the higher the root biomass share on the whole tree biomass is. The division of the root biomass into various depths is really interesting. E.g. *Quercus* family concentrates 90 % of the total root mass up to the depth of 1 metre and 70% up to 40 cm. In case of conifers, the 30 cm surface level concentrates 80–90 % of the root biomass. Generally, the surface horizon of about 40 cm in forest sites is considered a zone of intense rootage. However, in urban conditions, this depth needs to be greatly regulated, even due to the intense soil compaction.

4.2 Root functions

The root as an integral part of the plant organism holds the following functions: **anchoring** the plant in the ground or adhering to the ground (**mechanical** function), **occupying** new area by the root growing, **uptake of water and mineral** sources, **direct influence on the rhizosphere** (material flow and direct control of conditions of the symbionts development), **disintegration of the rock, soil protection** from erosion. It also **aerates** the soil and **enriches** it with organic materials (due to root turnover, i.e. dying and replacing with new ones).

Other essential functions involve the **conductive function** by transporting water enriched with diluted mineral substances and gases, the **storage function** (starch, mineral nutrients, water), the function of **specified metabolism** (esp. synthesis and excretion) and **information function** (hormonal activity – root as a growth and accumulation signal affects the production of photosynthates); **protective** function and **reproductive** function (root stools) and the **competitive** function in view to other organisms (root grafts, allelopathy etc.); it even has parasitical functions (haustoria). If some of the functions prevail, the root inner structure as well as the general shape may metamorphose.

4.3 Root zone activity (primary growth)

4.3.1 Meristem zone of the root primary growth

Roots grow in length on the root tips due to the **activity of the initials** of the **apical meristem**. The initials of the rest centre demonstrate low dividing and metabolic activity. New cells of the root cap, responsible for covering and protecting the root tip, are divided on the distal surface of the rest centre. At the beginning, the **root cap cells** are intensely divided, then they demonstrate a very intense metabolism and gradually reach the edge of the root cap to peel off. **Cells in the central part** of the root cap contain cascade **amyloplasts**. The change in their position tells us about the direction of gravity. The cap excretes **polysaccharide mucus**, which makes it easier for root to penetrate into the soil, protects the meristem from an injury, drought or from separation from soil particles. It also controls the uptake of ions into the root and supports the development of the microbial flora and mycorrhizal fungi.

Cells of the resting centre divide their own initials of the apical meristem on the proximal surface. By dividing (periclinal and anticlinal) the number of layers of root cells is increased as well as the number of individual layers cells. This zone cells only

have primary walls, they are interconnected with plasmoderms and have juvenile development features. A weakly developed membrane structure does not allow for high speed of respiration, any differentiated xylem is absent. There are **two main functions** of these cells: firstly, **cell dividing** as a precondition of the elongation growth of the root, and, secondly, **secretion of mucus** enabling the penetration of root into the soil.

4.3.2 The elongation zone

Cells divided from initials (derivates) **undergo division as well as primary growth in the elongation zone**. The higher the number of cycles that cells complete, the shorter they become in the end, and vice versa. Yet, not all parts of the elongation zone divide at the same rate. This e.g. leads to developing many more epidermis cells than vascular elements, related to the length unit of root. The heterogeneity in cell division rate and derivates growth determines further histological and functional root heterogeneity in the radial direction.

Water flow into vacuoles, containing glucose and fructose, is intensified, vacuoles grow in size and fuse into a central vacuole. During the **expansion**, this vacuole **develops a pressure** from the inside of cells **on the cell wall**. Their structures get reorganized – polysaccharides split, new chains of cellulose as well as other substances of cell walls are synthesised, such as hemicellulose, pectines, and even some proteins. Not only the uptake of water is increased in the elongation root zone, but also the uptake of nutrients – a part of whose gets accumulated and another part gets utilized.

Cell elongation develops pressure in a distal direction on meristem as far as the root cap, and in a proximal direction on differentiation zone cells with solid tissues. It is this pressure on the root cap that **allows root tip to penetrate into soil particles**. At first, roots grow through soil macropores (diameter over 0.1 mm); in **case of a risen soil resistance** (compacted, sandy soils with the majority of pores below 0.001 mm in diameter) the **secretion activity of the root cap grows** substantially. The period of root elongation depends on concrete species and it mainly occurs in early spring when the soil has gone over the frost, and in late autumn. Daily growth of roots varies greatly – it can be as little as 1 mm in *Acer saccharum* to as much as 56 mm in *Robinia pseudoacacia*. It is clear that a substantial role is played by the physiological age of a tree. It is obvious that in young, newly planted trees the growth is much faster than in the ones with well developed root system.

4.3.3 Differentiation zone

A process that has begun in the meristem is finalized in the differentiation zone. The outcome of this process is shape and functional differentiation of cells and tissues. On the root surface, there is a tissue called **rhizodermis**, which is a single cell layer with **no cuticle** or **stomata**. The cells are rather thick from the exterior tangential plane – there is a **mucus layer** on the surface, and a cellulose layer from the inside. **The mucus** is not a secretion output as in the case of calyptra, but it **is a part of the wall**. It contains a lot of negative ions and is enriched with microbial substances that are important in an exchange of cations between soil colloids and the root.

Rhizodermis has a special capability of **enlarging the surface** by the creation of **root rhizins**; this takes place roughly at the same distance from the apex as the first functional differentiated elements of xylem. Rhizin is **responsible for a uptake of**

nutrients and for a mechanical support. Such a rhizin activity is not as usual and intense in trees as in herbs, the rhizins are shorter and sparser, but they have longer lifespan than in herbs. It **entirely lacks in unfavourable soil conditions**, esp. weak aeration, **or if a root is occupied with mycorrhizal fungi** which fully compensate the rhizin function. Older rhizodermal cells and rhizins suberize, peel off and are usually replaced with secondary cork.

Under the rhizodermis, there is **primary cork** – much thicker in root compare to the central cylinder – except for e.g. *Vaccinium* which is single-layer. Primary cork of trees is made of **mesoderm**, often containing wide intracellular spaces (**aerenchym**) developed mainly in **wetty soil conditions** and a lack of oxygen. **Exodermis** is not formed in many cases at all. Besides the aeration function, the **primary cork** parenchyma also has the **following functions**: **storage** function (starch, proteins, lipids), **excretion** function (accumulation of tannin, mucus, ether oil and crystals), **protective** function (accumulation of toxic substances and detoxication of these in vacuoles), **synthetic** and **transport** functions. All these functions are partly held by **mycorrhizal fungi that live and develop in mesoderm**. A lot of substances like water, nutrients and gases, e.g. carbon dioxide or oxygen are transported from the soil through these cells through the **apoplast** – by diffusion through permeable cell walls and intracellular areas and by the **symplast** – through life cell bodies.

Endodermis cell walls are suberized and lignified in the radial and transversal directions (**Casparian strips**). These strips **prevent from further transport through the apoplast** so most transported matters have to cross the barrier of semipermeable membranes (plasmalems or tonoplast) and enter the symplast. The local **suberination and lignification** of cell walls **is only absent with permeable transfer cells** located opposite xylem groups of the central cylinder. Roots that demonstrate secondary diameter growth retain rhizodermis and primary cork only temporarily, they can be found in fine roots and the youngest parts.

The term **central cylinder** stands for a column of **conductive tissues** system inside the root, on its periphery bordered with **pericycle**. In more primitive gymnosperms the pericycle has multiple layers as a whole, or multiple layers may only be set locally opposite xylem and phloem groups. The **pericycle cells retain the capability to divide** – they take part in regeneration processes, they are **a formation place of lateral roots** and **part of cambium**, sometimes even **phellogen**. Their cell walls are penetrated with plasmoderms securing a contact between cells from endodermis and parenchyma in the central cylinder. The conductive system in root is represented by a complex **radial vascular bundle** whose individual parts of protoxylem and protophloem are arranged in rays. Phloem and xylem sections alternate. Based on the number of phloem and xylem groups, bundles are categorized into **monarch, diarch and triarch** (gymnospermous and dicotyledonous) and **polyarch** (monocotyledonous; palm trees, Monstera). Nonetheless, this rate may vary even in just one individual, such as the case of *Picea albies* with diarch, triarch bundles and monarch vascular radial bundle in its short roots.

Nearest to the root tip (0.1 – 0.4 mm) there are differentiated elements of phloem that take photosynthates and required K^+ into the system. Further away from the root tip, in an area where a root starts to operate as an organ absorbing water and nutrients, there is xylem. In *Abies* fast growing roots it is located 7 mm from the apex, in *Acer* in inadequate conditions it is only 0.2 mm. At first, xylem and phloem groups are arranged radially and their number is unstable. **Xylem** is differentiated in centripetal direction (exarch): **protoxylem elements are closer to the perimeter of the central cylinder**, and **towards the centre there are metaxylem** elements and there is

usually no pith. **Conductive pathways of wood** (especially vessels and tracheids) **act as dead elements**. Intense synthesis of cell wall substances (cellulose, hemicellulose and lignin) is active in their protoplasts during the elongation and differentiation. After the construction of these is finished, protoplasts disintegrate. **Substances released at the programmed death of these cells become part of the whole transpiration flow** and enrich nutrition of the above ground system.

Roots get branched behind the differentiation zone: **root primordia** are initiated endogenously in pericycle. Because of this, they do not have an effect on the structure of the conductive system of the parent axis, as they do in the case of stem.

When growing they tear the outer tissues of the root till the soil is reached. Even roots with suberized surfaces demonstrate a relatively high uptake of matter at places of root branching. Root branching multiplies the number of root tips, allows for a higher density of rootage and more intense utilization of a suitable soil area.

Apical, distal parts of roots are the most active parts in terms of synthetic activity, impact on rhizosphere, water and nutrients enriching from the soil.

4.4 Secondary growth and root functions

Roots of a tree grow into the depth by means of **two types of lateral meristems**. We can think of them as single layer shells of concentric cylinders. In the case of gymnosperms and dicotyledons, **cambium** is initiated in the central cylinder (proximally from the apex).

The first primary parenchyma cells that undergo the remeristemation are **located at the inner side of the primary phloem, then on the boundary between phloem and xylem groups and after that in the pericycle**, located at **outer sides of primary xylem groups**. Cross sections show that the layer of cambial cells could be oval (diarch roots), triangular (triarch roots) and so on in their early stages. Ensuing from the fact that cambium cells gradually divide mother cells of secondary xylem centripetally, mother cells of secondary phloem centrifugally and cells of secondary phloem-xylem rays between bundles in both directions, **cambium generally becomes of a circular shape** on the cross section (**Fig. 16**).

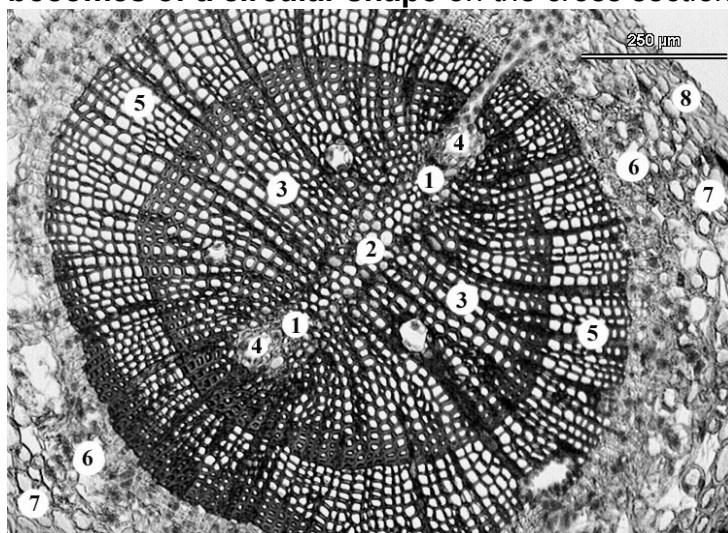


Fig. 16 Cross-section of Norway spruce fine roots. Vascular bundle was radial (diarch) at the early stage of fine root development. Primary xylem (1 – protoxylem and 2 – metaxylem); 3 – secondary xylem – first grow ring; 4 – resin ducts; 5 – secondary xylem – second grow ring; 6 – secondary phloem; 7 – pericycle; 8 – primary cork

Cambium in roots is active at different time in a year than cambium in the above ground systems. Cambium may demonstrate **different activity even among roots** in one individual. The same may happen even within one root – in one root part, it may be more active than in others. This is mainly due to mineral components present in the soil. **Root diameter increase in heavy and sandy/rocky soils is irregular**; most roots incline to develop eccentric structures, which further limit their conductivity. **Annual rings** in roots **are thinner** than in stems, they are **hardly visible**, and a typical clear layer of early vessels is missing in the ring porose ones. The proportion of individual elements of xylem in roots rather differs from the ones in stems and branches. The **secondary xylem** in roots can be **characterised by intense development of conductive pathways** (vessels and tracheids) and by a **higher content of parenchyma**. This allows for **easier transport and storage** and it supports the active participation of roots in the processes of material exchange. The number of **xylem fibres is reduced**, except for the ones in anchor roots and the ones with high mechanical requirements. **In general, cells in roots are bigger** than in stems and trunks; in tangential and radial direction as well as in length.

Phloem conductive pathways remain active or dormant in winter, but they usually **degenerate** as early as the end of their **first growing season**. In spring, new phloem elements differentiate from derivatives of cambial initials, having overcome winter in an imperfect state.

Along with a diameter increase of secondary roots, another secondary meristem, called **phellogen**, is formed. It is made by the remeristematic of pericycle cells. Secondary meristems and their derivatives could react to changes in the root environment. For instance, **if aeration is reduced**, abnormal xylem and phloem with an **increased content of parenchyma** are formed, transport of carbohydrates is inhibited, absorption of macrobiotic nutrients is reduced, root metabolism is limited. For example, **hypertrophied lenticels** are formed and the generation of **adventitious roots** is supported in some species (*Salix alba*).

Even though the **secondary root structure** may considerably limit the intensity of **nutrient uptake** from the soil, the total uptake is not insignificant compared to the activity of root tips. Although secondary roots have suberized surfaces this surfaces have fewer, thinner and more permeable layers than in the above ground system. Moreover, they are connected with the conductive system through phloem-xylem rays. Other locations with an intense exchange with the soil include **disturbed areas** of suberized surfaces near lateral roots initiations. Regarding that the total surface of suberized roots is very large, the uptake of soil solutions through this structure could not be omitted. If roots are uncovered and exposed to air for a long time, their bark or rhytidome resemble bark of a trunk both in the visual and functional aspects. Such roots lose the uptake ability and they mainly function is mechanical support and conductivity.

4.5 Mycorrhiza

The term mycorrhiza (from Greek *mycés* – fungi, *rhizó* – root) refers firstly to root symbiosis of higher plants with soil microscopic fungi, secondly to organs formed during the symbiosis of a host plant root and an endophytic fungus. The latter is mainly used in ectomycorrhizae, in which the association of a root with a mycorrhizal fungi substantially affects morphological and anatomical root structure.

Mycorrhiza are the most widespread symbioses that roots of plants create. Foundations of plant roots fossils indicate that the predecessors of present fungi forming vesicular-arbuscular mycorrhiza lived in the symbiosis with plant roots as early as their expansion from water to land environment, which dates back to approx. **350 – 460 million years** (from the Ordovician to the Carboniferous periods). Other mycorrhizal types are younger and more derived.

One of **typical features of mycorrhiza** is that their **development in roots of host plants is only limited to the primary cork** of roots. Mycorrhizal fungi never appear in the central cylinder. Another distinctive feature of all types of mycorrhiza is a **formation of a network of mycelium in soil**, not in roots. This extramatrical mycelium, functioning mainly as a satellite of a plant root system, substantially enlarges soil volume as a source of nutrients, esp. phosphate ions, to the plant.

Based on the latest monograph dedicated to mycorrhizal symbiosis, the following basic types of mycorrhizae are distinguished: orchideoid, ericoid, arbutoid and monotropoid. The older categorization into endomycorrhizal and ectomycorrhizal symbiosis related to the **capability of a mycorrhizal fungi to colonise cells of primary cork. Only the endomycorrhizal are able to do this.** The development of an endophytic fungus in **ectomycorrhizae is limited to intracellular spaces** in primary cork. In this aspect, ectendomycorrhiza, arbutoid and monotropoid mycorrhizae are a transitional type –fungus colonises primary cork cells, but these mycorrhizae have some common features with **ectomycorrhiza**.

The following text describes only the types of vesicular-arbuscular mycorrhizae, ectomycorrhizae and ectendomycorrhizae as these are the ones that play the most important part in woody species.

4.5.1 Vesicular-arbuscular mycorrhiza (VAM) = arbuscular mycorrhiza (AM)

VAM includes a really wide spectrum of species of host plants – it is estimated that about 80% of all plant species form this kind of mycorrhiza. In this view, it is the **most widespread symbiosis** in the world. It can be found in plant species through all climatic zones and environmental conditions, no matter if they occur with trees, bushes or herbs. Typical woody species that form VAM are from *Cupressaceae* and *Taxaceae* families; VAM also occurs in seedlings of *Pinaceae* family, though this family usually forms ectomycorrhizae.

No species-specific VAM symbiosis has been documented yet, so, it is generally presumed that there is no such specialization. In a different manner, there has been an evidence of a certain kind of environmental differentiation. It lies in the preference of certain fungi species by different plant species in the same environmental conditions.

Typical structures of this type of mycorrhiza **are arbuscules**, alternatively vesicles, whose presence makes the background for the most widely accepted definition. **Arbuscules are formed inside cells** of a root primary cork. They could be **characterized by their multiple fork-like branching** and finalized growth. Arbuscule cell wall is thinned or absent. The plasmatic membrane of a fungus is never in a direct contact with cytoplasm of a cork cell. Arbuscules are considered to be the centre of symbiotic transmission of phosphates and carbohydrates between a fungus and a plant. **Vesicles are located either inside root primary cork cells or in intracellular spaces.** They have a **storage function**, containing mainly lipids.

4.5.2 Ectomycorrhiza (EM)

In comparison to VAM host plants, the number of **EM host plants is very small** – it only makes up about **3%** of species of all plants. Yet, this is an especially **significant type of symbiosis in our tree species** as it appears within families *Pinaceae* (especially *Pinus* and *Picea*) and *Fagaceae* (*Fagus* and *Quercus*). Another important families with EM are *Myrtaceae* in subtropical and temperate climates in the southern hemisphere and *Dipterocarpaceae* in the monsoon forests in the South East Asia. Even other species of other families form EM (e.g. *Betulaceae*). **Some species can either form VAM or EM**, depending on soil conditions of the site. Such families include *Eucalyptus*, *Salix* or *Populus* – EM is formed in conditions of very humid soils.

Compared to VAM, when the creation of mycorrhizal association does not affect morphology of an infected root, the **formation of EM symbiosis leads to substantial changes in the structure of root tips** (only these are capable of EM formation). Their apical meristem finalizes its growth so **root is shorter and thicker**. The extent of the shortening and thickening processes depends on the development stage of a root tip at the moment of its contact with a mycorrhizal fungus. Another typical feature is forked root branching. **An ectomycorrhizal root has several fold longer lifetime** (approx. 3–4 months) than a non-mycorrhizal root tips.

The following structural components are typical for ectomycorrhiza:

- 1) **Fungi mantle** – it covers root surface. It may only be weakly developed or absent. Typically the biomass of a fungus mantle makes up of 20 to 40 % of the total biomass of a short EM root.
- 2) **Hartig net** – a labyrinth of hyphen growing from fungus mantle into the rhizodermis and intracellular spaces of root primary cork. It is typical for these hyphen to be branching intensely. Spreading of hyphen may be only limited to rhizodermis, (typical for angiosperms, or they may grow in intracellular spaces of more layers of the primary cork, they sometimes might grow through all layers of the primary cork (typical for gymnosperms). **Hartig net is a place of the most intense material exchange between associated symbiotic organisms.**
- 3) **Extramatrix mycelium** – serves to absorb nutrients. It may be aggregated into rhizomorphs, i.e. thick strands of hyphen, that are clearly visible. **Rhizomorphs serve to transport material on long distances.**

Older studies regarded fungus mantle as a centre of uptake of nutrients from the soil. Nonetheless, at present, the extramatrix mycelium is considered to take an essential part in the absorption of mineral substances as in the case of other types of mycorrhizae. The Hartig net is a place where minerals absorbed from the soil are exchanged for carbohydrates assimilated by a plant in the photosynthesis.

Ectomycorrhiza is mainly formed in the soils rich in organic substances, especially surface horizons of forest soils. A substantial portion of phosphates and other nitrogens in these horizons may exist as organic compounds. EM fungi are able to disintegrate these organic compounds by means of hydrolytic enzymes, and perhaps even due to associated bacteria. Acceptable mineral forms of nutrients for plant are formed.

4.5.3 Ectendomycorrhiza

Although ectendomycorrhizae are **quite widespread**, we **do not have** much reliable **information** on them. They could be formed by woods that commonly form symbiosis with EM, especially in the early ontogenetic stages (described e.g. in

Pinus, Larix, Picea). Some fungus taxons with active ectendomycorrhiza are related to EM fungi, as well, since these may form a typical EM, depending on a host plant. All aspects of development and formation of typical structures are comparable to EM, except for the intercellular penetration of primary cork cells of a host root. **Both fungus mantle and Hartig net are created**. And, at the same time, **hyphen grow through primary cork cells** where they are intensely branched. This symbiotic association is very stable, and, similarly as in EM, roots do not demonstrate any traces of senescence.

4.6 Metamorphoses of root

In the course of evolution, root functions have changed considerably in many instances. This concerns all types of roots – main, lateral or adventitious. Along with the change in function, the shape and inner structure have changed, too. Root metamorphoses may be so enormous that the original character of this belowground structure has gone completely away.

Many adventitious roots of species located in loose or muddy soils fulfil mechanic functions. It is as if plants were standing on stilts, that is why these roots are called **stilt roots**. The same function is also taken by so called prop roots that support giant trees of many tropical species, and **buttress roots**, developed in some species in tropical rainforests. Many lianas, e.g. local Ivy (*Hedera*) and numerous epiphytical species are **fixed by adventitious roots**. The fixation function is also made by adventitious roots, formed on stems of creeping species, e.g. *Cotoneaster*, *Salix*, *Pinus mugo* and the like. A plant uses them to be tied to the soil, and at the same time to take in nutrients. They can even be separated by means of the **vegetative reproduction** an form a polycormons. Some **spines** on palm trunks originate from a root.

Aerial roots commonly appear with epiphytes. They grow freely in the air and **their dead cells** of multilayer rhizodermis **absorb water from the rainfall**. Such roots may also have the **assimilation function**. Species that live in wetland areas with a lack of air have breathing roots, **pneumatophores**, that mediate an exchange of gases. They grow right up in the air, their tips stick out of the soil or water (*Taxodium distichum*).

Parasite roots (haustoria) are special case of metamorphoses. Some lateral roots develop as tiny tubers. Haustoria, meaning organs that draw nutrients from a host plant, grow from the tubers and penetrate as far as vascular bundles of a host (*Viscum*, *Loranthus*).

4.7 Limiting factors of root system growth and functions

Firstly, these are the factors that reduce the positive carbon balance in the above ground system (i.e. balance between the photosynthesis and respiration) or negatively impact the translocation of photosynthates and growth hormones in a different manner: **radiation stress, temperature stress, water stress, intoxication, injury stress** (by an intentional cut or by the wind, snow, frost), **oxidation stress** (by increased entry of oxide substances such as O₃, SO₂, NO_x, PAN etc.), **damage to conductive pathways and tissues** (by frost and bark scarlatina of unshaded trunks), **by fungi, viruses, insects and a range of other negative factors** including the ones that are connected with various defoliations.

Other important factors include **soil factors**, especially the soil type, into which roots penetrate and regenerate. Further, it is a **high content of skeleton** (rocks, stones, remainders of brickwork etc.) and the mechanical impedance of soil that limits the root penetration. The soil in urban areas is commonly **compacted** (by walking, driving of heavy machines) and **flooded** (as water from rains cannot easily get absorbed). If soil aeration is limited (**hypoxia**), this leads to a higher production of potentially toxic materials, to the modification of shoot growth, inhibition of formation and growth of leaves. When this affecting is long-term, the diameter growth of adult trees slows down, and the phloem and xylem anatomy gets transformed. In such cases, the **absorption of minerals is limited due to a smaller extent of the root system and a lack of energy**. This is because of the fact that in the anaerobic respiration of an organic substrate, less energy is released than is required to cover the needs of complex root functions. Not only the soil drought, but also hypoxia may stop the uptake of nutrients and it may even happen that **ions are released from the roots out into the soil**.

The **soil drought** results into a worsened uptake of water by the roots, transpiration and assimilation limitation (i.e. worse cooling of leaves, supply of leaves with nutrients and roots with photosynthates). Moreover, it results into the efflux of nutrients in fine roots and into the limited contact of roots with the rhizosphere, and may end in death of roots. The soil drought together with **unfavourable atmospheric conditions** such as low relative humidity, high temperature or wind; generally the ones that lead to an increased evaporation, might bring about a **damage to the conductive pathways** in xylem by high negative pressure. This may cause breaking of water columns and a consequent suction of air or cells (from the neighbouring parenchyma) into the vessels.

Fine roots mortality may also rise due to a **high content of salts** in the soil, due to an imbalanced uptake between individual nutrients, **low recoverability of nutrients and an absence of mycorrhizae**, winter starvation, summer temperature (thermal convection of asphalt surfaces, thermal radiation of buildings etc.).

One of ways of sustaining trees in towns is **to secure them conditions needed for their well being**. This means to make a range of tasks, namely to secure long-term good quality and volume of the belowground and air space, and to regularly secure their requirements for water regime (irrigation, evaporation), temperature regime (planting in groups) and light regime (i.e. to respect demands on density and quality of radiation, length of day and growing season, sum of radiation in a growing season and in a calendar year) and to regularly manage natural soil processes (i.e. mainly the recoverability of nutrients and the presence of suitable soil flora and fauna).

In confined urban spaces such as pedestrian zones or stations of public transport etc., trees are often **placed into special containers** on the ground level **covered with decorative lattices**, serving as prevention from the soil compaction by walking. These lattices should be made of modules dismountable in the radial direction (in case of a round container) as well as the tangential direction (links between partial circles). Such a treatment is especially required by the base part of a trunk, since the volume changes in the diameter growth are really great at this place. The same is true for volume changes in the root system due to the elongation growth. The base part of a trunk may quite soon reach considerable volume changes at the places of connections of roots with a trunk, which are of a high importance for the mechanical support of a tree. The ground level containers have the following disadvantages: **easy entry of salt water** from melting snow and ice removed from roads. The salt

solution in winter has a much lower temperature than the soil, which means that it may promptly and repetitively contribute to **freezing out of fine roots**.

In the urban zones, trees are also held in **above-ground containers** placed on the surface of streets. They have these great advantages – the soil is protected from dirty salt water and from being walked on. On the other hand, the soil is **not protected from the frost** at the beginning and end of the growing season, or from **overheating and drying** in summer.

5 The stem

The stem (caulom) is a vegetative, usually above ground structure with nodes. It generates, differentiates and holds lateral branches, leaves, flowers and fruits. The stem mediates their connections with the roots by distribution of water, nutrients, photosynthates, and material, electric and stress information signals etc. It participates in photosynthesis, defence and protection, its directed growth occupies the optimal space and it is a storage of water and starch for overcoming bad periods. The elongation growth, generation of leaves and lateral branches is made by the apex meristems. The connection of these new modules to the roots is secured by the cambium. A significant role of a stem is also to maintain spare suppressed buds that can renew growth after a heavy stress, e.g. after an injury by wind, lightning, browsing, frost, drought, starvation etc. Some other important roles include vegetative reproduction or holding a plant on the spot.

Internodes of a stem are sections between two nodes, which are a base of leaves and buds. **The length of internodes** corresponds to the biological type of a plant (**longest in lianas, shortest in gymnosperms** – on shortened shoots holding bundles of needles – **brachyblasts**), to the **age and position** in a tree crown (e.g. quickly growing seedlings after a deep reduction of a tree crown compared to edge parts of crowns of old trees), environmental condition (shaded stems demonstrate a lower length of internodes than stems in the direct sunlight). **A tree stem with leaves is called a shoot.**

An unbranched part connecting the root and the tree crown is known as a **trunk**, stems within the crown are called **branches**. Trunks usually have the radial symmetry, the most frequent shape is cylindrical, but may also be muscular, flattened etc. At the bottom, it is extended by roots. By the direction of growth and self-bearing capacity, stems are categorized into different groups: direct (heliotropic – grow up vertically, plagiotropic – grow horizontally, bent when older and grow down), overhanging (pendular), ascending, lying, creeping (cotoneasters), supporting (blackberries) etc. Trunks are among the greatest organs in the plant kingdom. Palm *Calamus* (leaf-climbers) might reach as high as 300 metres. The tallest trees reach up to 150 metres. These are Australian eucalyptus which are even taller than sequoia (*Sequoiadendron giganteum*), reaching 120 m. The greatest circumference has Mexican Cypress (*Taxodium mexicanum*). With the diameter of 31 m it wins over North American sequoias. Nonetheless, sequoias still hold the world record as the largest organisms by volume.

The **stem structure** is made of **covering tissues, primary tissues, conductive tissues** differentiated from the apex meristems. In this case, the **epidermis** on the surface is a single layer (sometimes with well developed stomata), it has commonly a **cuticle and trichomes**. In a **multi-layer epidermis** tissue, layers below the epidermis are called the **hypodermis**. The **primary cork** lies under the epidermis

and consists of two to three layers – upper layer of primary cork has a mechanical function. It contains collenchyma, commonly with chloroplasts (in young stems it quickly loses its tension (turgor) when water is absent). The medium layer is usually parenchyma with the assimilation function. The lowest layer is made of living cells of **endodermis or its cells of another kind**, such as starch stripes, but it could be also absent. The **primary cork has mechanical, storage, assimilation and protective functions..**

Closer to the centre, there is a **central cylinder**. On its periphery, there is a **pericycle** (latent, secret meristem where adventitious roots and buds may originate), below, there is a system of conductive tissues, i.e. **vascular bundles**. There are **two types of vascular bundles** in stem of **gymnosperms, dicots and monocots (Fig. 17)**. The **first lead from the stem to leaves**, the other **run through the stem individually**. In **monocots, all vascular bundles are leaf traces**. In case of conifers and angiosperms, the vascular bundles are collateral, arranged in a circle. On the cross-section they create a circle surrounded by the primary cork at the outer side, and by pith at the inner side. Pith is connected with primary cork by stripes of parenchyma tissues, pith rays.

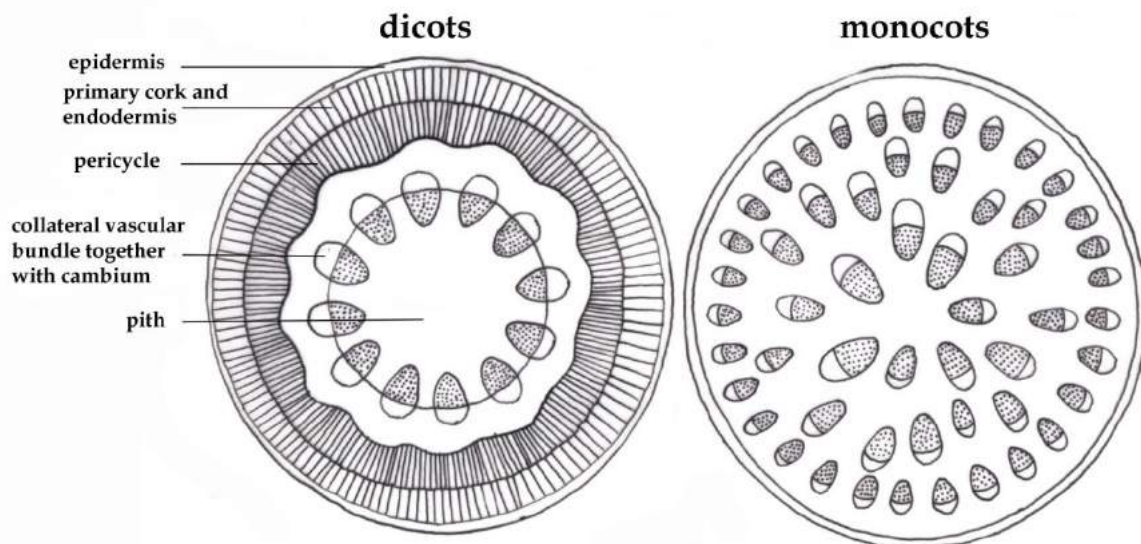


Fig. 17 Vascular bundles arrangement in gymnosperm and dicots (left) and monocots (right).

Stem pith fills the centre. It has thin walled cells, most commonly freely connected, cell wall is sometimes weakly lignified. Intercellular space in pith are filled with air or water. Pith of some trees quickly breaks (*Juglans*, *Vitis vinifera*) and new cavities are formed which are interrupted by partitions. While in some species, pith is sustained for a long time and functions as an assimilation tissue (ash tree), in others it dies after the first year, e.g. elderberry bush.

5.1 Secondary growth of stem

Secondary growing stems gradually **develop a secondary structure** depending on the formation and activity of secondary meristems (Fig. 18). These include **cambium**, which replaces the systems of conductive tissues divided into phloem and xylem sections of vascular bundles, and the systems of primary tissues with phloem-xylem rays, and resin canals in gymnosperms such as spruce or pine. We distinguish between two types of cambial initials in woody plants. Cambial initials are named **fascicular cambium (form xylem and phloem)**. The second type, **interfascicular**

cambium (form pith rays), is usually formed at the end of the first year. Fascicular and interfascicular cambium together make a continuous cylinder on the cross section. Another secondary meristem is **phellogen**, which generates secondary covering tissues, i.e. secondary bark.

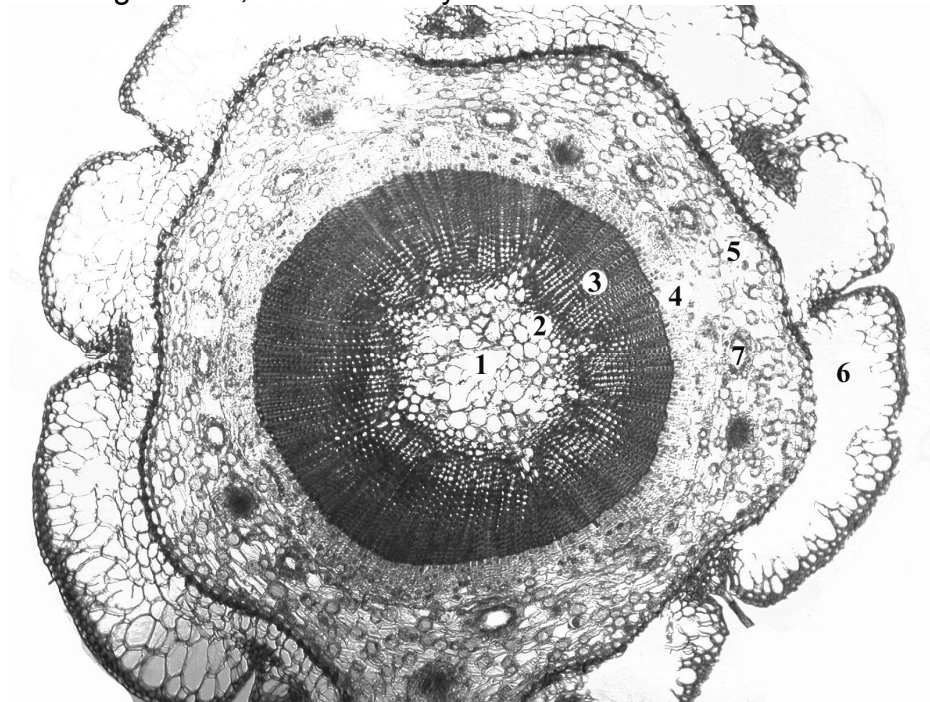


Fig. 18 Cross-section of one-year old Norway spruce shoot. 1 – pith; 2– primary xylem; 3 – secondary xylem; 4 – secondary phloem; 5 – pericycle with resin ducts; 6 – primary cork; 7 – resin duct

5.2 Development of annual rings

Cambium activity depends on the activity of meristem cells of the stem apex, lateral buds, signals from leaf, roots and suppressed buds. It begins **in spring** by first dividing and differentiating of **phloem and xylem mother cells** that were formed in the previous **autumn and survived winter**. Cambial initials take water into vacuoles, their thick cytoplasm is pushed by the growing vacuoles to the wall which is extending and becoming thinner in the radial direction. This **action begins below buds** due to the phytohormonal factors (auxins, gibberellins, cytokinins with co-working of carbohydrates).

In the case of the diffuse porous woody plants, this activity **directs from stem tips towards the trunk base**. If **ring porous** woody plants are considered, this process **begins later, but is faster**, and as early as the first buds begin growing, the first vessels are functional. Regarding conifers, the impulse comes from old as well as new needles. Dividing of cambial initials begins a couple of weeks later, the division spreads all over the trunk and the process **ends in the root system**. The same process applies for closing of cambial activity in autumn, and this is why roots grow even in autumn.

The **first cells produced by cambium** in spring are **xylem** mother cells, **phloem cells follow**. In this period xylem cells grow really quickly and their cells have larger lumen and thinner walls. Such wood is important for its **conductive function**. In **summer**, the situation is reverse. Cambium activity slows down and latewood cells are thick-walled; they have **mechanical and defence functions**. So this is how **early**

and late wood originate – its annual growth is known as an **annual ring (Fig. 19)**. However, there are cases when more than one annual ring may be formed in a year. Such **false rings** come from a defoliation of a tree (e.g. by insects), interruption of the growth activity (e.g. by drought) and due to other unfavourable factors. The activity of **phloem formation** is weak in spring, but it sharply rises in the course of the growing season and continues till autumn. In spring, the cambial zone is thick (cells of initials with mother cells of conductive and primary tissues), in autumn, it is thin, on the contrary. Cambium activity in young trees starts earlier in spring and finishes later in autumn than in the case of old or weak trees.

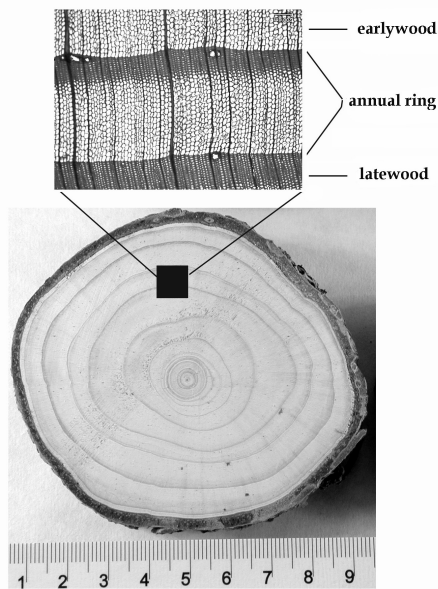


Fig. 19 Cross-section of 13-years old Norway spruce branch. Annual ring is formed by earlywood (conductive function) and latewood (mechanical and protection function)

5.3 Wood of coniferous species

It is an **evolutionary older type**. It can be characterised by a simple structure, typical alternation of **early and late tracheids and parenchyma cells (Fig. 20)**. These elements build the structure of annual rings. The main constituent of wood is **tracheid**, that makes up about **90% of volume of coniferous wood**. **Conductive function** of early tracheids reflects their shape – **thin walled, prosenchymatic cells**, length 2–6 mm and diameter 0.04 mm (wall thickness 2–3 μm). Water flows through **border pits** in the cell wall, which is why **coniferous wood is quite resistant to water flow**. Water is well supplied due to an increased rate of early tracheids – trees in good years form more early wood than late wood. The **wider the annual ring is the more early tracheids** are produced. Yet, tracheids fulfil the conductive function longer than vessels of deciduous species, and a larger part of wood is active in water transport (more annual rings). Late tracheids are **thick-walled**, sclerenchyma cells. They are roughly 10% **longer than early tracheids**, and cell wall is 3–7 μm wide. Another cell types are **parenchyma cells**. These are thin-walled, isodiametric cells that play a role in the formation of resin canals and pith rays. They fulfil **secretion functions**, secure **radial transport** of water and substances, they fulfil also mechanical functions.

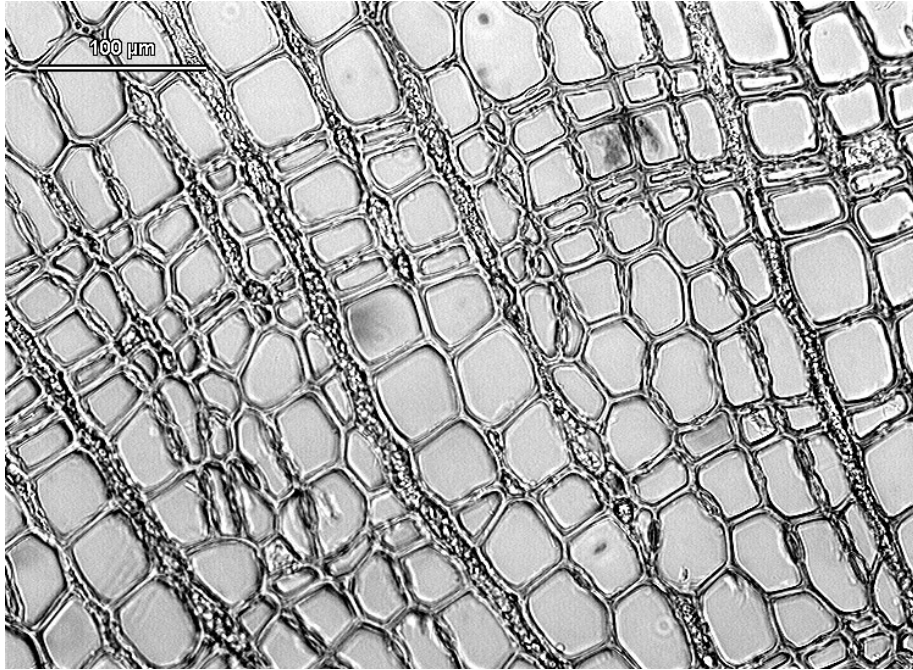


Fig. 20 Coniferous wood structure (*Picea abies*)

5.4 Wood of deciduous species

The wood of deciduous plants is **phylogenetically younger** than the wood of conifers. This is reflected in a **higher complexity** of the structure, a higher assortment of cell types, which are more specialized on certain functions. Deciduous wood is made of **vessels, tracheids** (fibre, vasicentric, tracheidal), **libriform fibres** and **parenchyma cells** (Fig. 21). **Vessels** are specialized conductive elements made of vessel elements. They may reach **considerable lengths** (5–18 m for oak, 0.8–2 m for birch). The most common **length is 10 mm**. Taking into account their considerably thin cell walls, **vessels do not have a high mechanical stability**. Therefore, they are **reinforced** with spiral or round thickening. Depending on species, the rate of vessels in the overall wood volume varies from 4–8 % (maple) to 22–48% (*Populus, Fagus, Fraxinus*). There are **three types of deciduous tracheids**: tracheidal, vasicentric and fibrous. The first ones mainly fulfil a conductive function and do not occur with the majority of deciduous trees. Vasicentric tracheids also have a conductive function, but only appear in company with vessels, such as oaks. Fibrous tracheids are cells with a mechanical function, but they can also fulfil conductive and storage functions. **Libriform fibres** are mechanical elements of wood of deciduous trees. Their percentage representation ranges from 36% (*Fagus, Tilia*) to 78% (*Acer*). These are thick walled, short, cylindrical or spindle cells. Their shape and size make them really stable cells that can secure the wood solidity. Parenchyma cells in deciduous cells make up about 8 – 35% of wood volume. They are tiny cells, mostly isodiametric, sometimes of a roll shape.

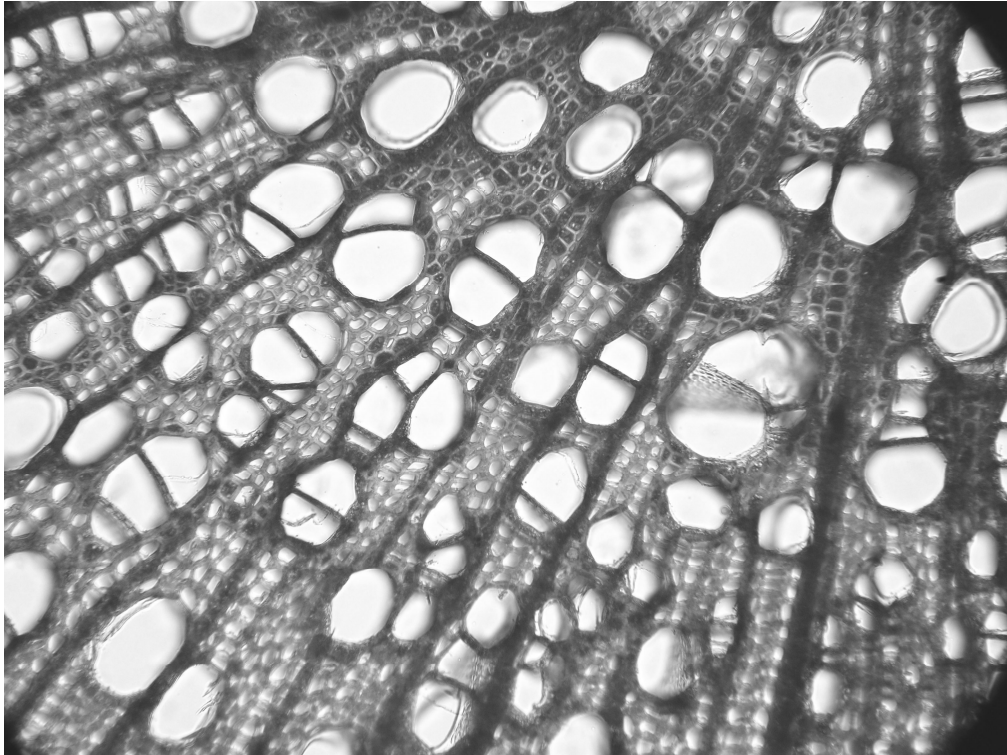


Fig. 21 Structure of deciduous ring porous wood (*Salix fluviatilis*)

5.5 Stem morphology

Trees have a distinguished **main stem, trunk**. It does not branch and usually **bears lateral branches and leaves**. **Skeleton branches** (branches of the first class) bear **macroblasts** (branches of the second and higher classes). Shoots with shortened internodes are called **brachyblasts**. In some species, they are formed regularly (*Ginkgo, Larix*), but in most species only as a modification which allows for the annual generation of new leaves, flowers and fruits without extreme growing of a crown (*Tilia, Fagus, Malus*). All branches make a crown. It gives trees their typical appearance – habitus, depending on means of branching, number of branches, direction of branches, foliation etc.

Monocotyledons have enclosed vascular bundles, they are scattered and all of them pass from stem to leaves; there is no boundary between the primary bark and the central cylinder, there is no pith or rhytidome. **Secondary thickening is rare** (does not exist in palm, bamboo). It is carried out through cambial initials centrifugal dividing of primary parenchyma tissue (gradually sclerifying) and individual vascular bundles. The phellogen is formed on the outer side, dividing cork, with an occasional occurrence of parenchyma and sclerenchyma cells (aloe, dracaena, yucca).

Branching of tree stems is holoblastic (apex tip does not split, it remains as a whole complex). There are two types:

1. **Monopodial – racemose**. The main apex is the tallest, lateral branches are shorter. It is thicker and its individual modules are derived from the original apex tip.
2. **Sympodial branching**. The main apex is the shortest and lateral branches are taller. Sympodium is further classified into:
 - a. **monochasium**, formed in **woody species with alternate leaves** and node buds. At the end of the growing season the apex growth slows down and the tip bud either remains under-developed or does not survive winter.

In late summer or the following spring, the nearest lateral bud gets into the position of the terminal and gives rise to a new main shoot. By growth of lateral branches of higher and higher classes, a branch elongates (*Tilia*, *Betula*, *Populus*). Monochasium is also developed in wine (*Vitis vinifera*), whose apex bud metamorphoses into a shoot. A lateral bud – based in a leaf node overtakes its leading position.

b. **dichasium** is typical of **woody species with an opposite position** of leaves and node buds. Even in this case the leading stem weakens as time passes, or the terminal bud differentiates as a flower. Then it shoots and there arise two almost equal stems of both opposite buds (*Syringa*, *Acer*, *Aesculus*).

Monopodial woody plants rarely retain this exact type of branching in their lifetime; they often pass to the other branching pattern. There are a lot of factors leading to this change, like injury, parasites, inadequate functioning of the root system, drought or age of an individual. **Monopodium remains** the main type of branching for a long time for instance **in spruce with a conical crown**. Yet, its branches incline to **sympodium**. Similarly, a crown in **young pine trees is monopodial**, but old pines crowns are not monopodial, which reflects in bizarre shapes of crowns. The sympodial branching, especially **dichasium**, forms **rounded and oval tree crowns** or conical and conoid crowns. The shape of a crown is more plastical and can better capture the sunlight and prevent from evaporation. On the other hand, if a dichasium branching develops too soon, two main skeleton branches may develop in the crown, whose phototropic growth (towards the sunlight) drives them apart, and this may end in a **huge break due to the opposite forces** of two large heavy branches. The tree crown, its size and shape are defined by the species and age of a tree, i.e. differences in rate of growth of terminal and lateral branches and type or branching. However, even **sunlight** (solitary crowns and individuals in related greenery), unidirectional dry **wind** (flag-like crowns) and low **soil humidity** (umbrella crowns) play a significant part in the final crown shape.

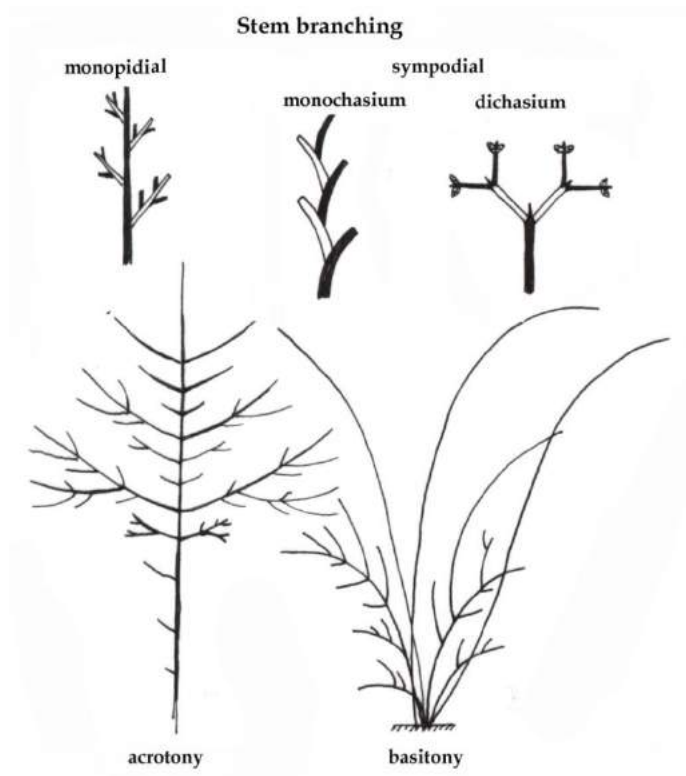


Fig. 22 Stem branching pattern and tree and shrub growth. Monopodial – the main apex is the tallest, lateral branches are shorter. Sympodial branching – the main apex is the shortest and lateral branches are taller. Acrotony – growth form of tree. Basitony – growth form of shrubs.

The **arrangement of leaves** on the stem, **phyllotaxis**, is defined by plant species. In the **opposite pattern**, leaves grow in pairs facing each other, turned of 90° from the lower node (e.g. *Acer*, *Aesculus*). If more than two leaves grow from a node, this pattern is called **whorled** (e.g. *Catalpa*). The position in more or less loose screws is called **alternate** (or spiral). In this case, some of the leaves are positioned in vertical lines (**orthostichies**). If we want to get from a given leaf to the nearest in the same orthostichy, we need to go round the stem several times and pass leaves of other orthostichies. **The number of round and leaves defines the type of a leaf pattern.** **Distichal** ($1/2$, meaning two leaves in one round, the third leaf in the same line above the first) is typical in shaded branches, such as in **beech, elm, lime and monocots.** **Dicots** bear leaves in the pattern $2/5$ (but also $3/8$, $5/12$ etc.). If the arrangement of leaves is modified by their light reaction, i.e. change of spacial arrangement e.g. as a result of a leaf mosaic, it is necessary to study the position of leaves in a bud to be able to define the type of phyllotaxis. The shape of stem pith relates to phyllotaxis.

5.6 Bud

The bud is the **foundation of a future structure (shoot, leaf, flower)**. It consists of apex tip meristems, leaf primordia in the acropetal order, and axil buds. The oldest leaves, sometimes metamorphed into scales, protect a bud.

Buds at the tip of stems (branches) are called **terminal buds**. This is the leading apex bud of the main stem or trunk. Buds in the axils of leaves, i.e. in stem nodes,

are **axillary, lateral buds**. The vertical arrangement of these is called **serial** (*Lonicera*), horizontal is called **collateral** (*Prunus spinosa*). Apex and lateral buds, i.e. regular buds in trees flowering prior to foliating, may be subdivided into **flower buds** bearing the base of a shortened stem and leaves modified into flower parts, and **leaf buds** bearing the base of a shoot. Undifferentiated buds are mixed, giving rise to shoots first and flowers later (*Tilia*).

The classification by the inner differentiation defines buds of the **fir and poplar type**. Regarding the **fir type** buds, the whole shoot foundations were based a year prior to spring when they begin growing in volume. Considering the **poplar type**, new shoots develop according to climatic conditions in the same year of shooting and growing, there is no significant role of the previous year.

The buds that are passive only for **one resting period** and start developing the following spring, are called **winter buds**. The ones that remain passive are called **dormant buds**. If these grow and branch, but still do not reach the surface of the bark, are called **suppressed buds**. This type enables the reproduction and regeneration of a wood plant when its integrity is violated, perhaps by the frost, fire, weak functioning of conductive tissues, age etc. The same function is held by the adventitious buds, formed beside the regular order on the internodes, nodes of a stem or roots. These **reserve buds** are commonly called preventive buds.

The inner structure as well as the outer appearance could be considerably modified or metamorphosed from the above described models if a stem takes over other functions, such as a defence function – **prickles**. Some species have prickles only in young individuals, or root sprouts or low branches, while they are absent in a crown. The climatic conditions play a part too, e.g. in blackthorn these structures only develop on dry and warm sites, while in humid conditions of a greenhouse, they do not develop at all. This is due to the fact that in this case thorns etc. are a protection from herbivore animals. **Assimilation (green) stems** have e.g. *Cytisus* and stems of succulents serve as **reservoirs of water**. Stems also secure **vegetative reproduction** when branches are in contact with the soil they might give rise to adventitious roots (*Fagus, Picea* aj.), which could later develop into individual plants.



Fig. 23 Leaves and axillary buds are formed in the first year. Terminal buds are formed when shoot elongation growth slowdown. Conifers form axillary buds only at the base of few needles.

6 Leaf

Leaf (phylum) is a lateral structure generated by the stem, it has a pre-defined position, limited growth and age. A leaf fulfils numerous **functions**: **photosynthetic** (i.e. reception of solar radiation, CO₂ and release of oxygen), **transpiration**, **conductive** (i.e. evaporation, cooling, control of cell tension – turgor, supply of leaf with nutrients and conduct of photosynthates away) and **respiratory** (i.e. respiration and renewal of precursors for syntheses – e.g. chlorophyll). Other significant functions include **reproductive** (type of leaves called **sporophylls** – microsporophylls and megasporophylls and flower phylloms) and **regulation** functions (phytohormones production). The most frequent, typical leaf is modified in order to optimally work at material exchange with the environment, and this is why its exterior as well as interior surface is large.

Besides, leaves can take over other completely different functions, which makes their structure completely modified, e.g. defence function by the modification into spines. Leaves are the **most variable organ** in an individual which ensues from its numerous functions and necessity to structurally react to different environments in a tree crown (light, wind, air humidity, temperature gradients). If a leaf completely changes its appearance and structure not as a result of the photosynthetic function, we call this change a **metamorphosis**. If it only reacts by slight deviations in the structure or shape to exogenous impulses in order to optimally fulfil the function it is called a **modification**.

6.1 Phyllogenesis – the evolution of a leaf

Leaf of vascular plants originated in a set of terminal plant body elements, sterile telomes of psilophyton plants. Telomes used to planate, flatten, adhere and develop in two directions. This is how large flat assimilation leaves, called **macrophyll**, of present ferns and angiosperms were formed. A **microphyll** (a needle or scaly leaves of angiosperms and meiophylls, thin single-vessel leaves of horsetails) is thought to have originated by the reduction and condensation of macrophylls or their elements. A flat leaf, found in *Ginkgo biloba* (i.e. among angiosperms) evolved from **grafted needles**. Broad leaves of Japanese umbrella-pine (*Sciadopitys verticillata*) evolved the same way.

6.2 Ontogenesis – the individual development of a leaf

A leaf develops on the apex tip as a leaf primordium. Further on, an axil bud develops in its axil (scattered in angiosperms, regular in dicots). Buds of some woody species (early flowering, e.g. *Acer*, *Forsythia*, *Magnolia*) divided by their origination into leaf buds (bearing leaf elements) and flower buds (bearing flower elements); buds in other species are mixed – first leaves grow, followed by flowers (inflorescence – e.g. *Tilia*) on the tip of the shoot.

In the mild climate of Central Europe, buds of nearly all woods are **protected by covering scales**. **Naked buds** (without covering scales) can be found in *Fragula* and *Viburnum lantana*, **semi-naked buds**, covered only at the bottom side, can be found in elderberry bush (*Sambucus nigra*). **Submerged buds** (covered only at the bottom of a leafstalk) are typical for *Platanus*. **Scales** that cover buds are formed in various ways (**opposite, double-line, spiral, sloping**), they are either bald or lashed, hairy, feltlike or veined (*Aesculus*).

The placing of a leaf in a bud prior to its opening is called the **vernation**. Woods may have a **flat vernation** – front sides of leaves are one on top of another (*Viscum*); or **compound** – if young leaves are folded in halves, each covered with the previous one (*Prunus*); **cirrus**, where the blade is folded in a cirrus matter along the main vessels (*Fagus*, *Carpinus*); or **coiled** (under or above). Besides the vernation, **estivation** is classified too. Estivation is the relation between leaves in a single bud which can **touch each other, be lied one on anther etc.**

Leaves on the stem develop **acropetally**, i.e. from the stem base with the oldest leaves towards the apex with the youngest leaves. The interval between the origination of one leaf and the origination of the next is known as **plastochron**. Regarding the evolutionarily **older plants** such as turf, cycas, a leaf grows by dividing of apex meristems. This means that the **apex part is the youngest**, spiral, **leaf base is oldest**, develops first. The **opposite** process applies to **conifers and gymnosperms** whose leaves grow by dividing of **basal meristems** – the **oldest parts are leaf tips**. In spring, leaf tips get damaged by late frost or salty solutions from urban and road salt treatment. In autumn, **leaf tips and edges are the first to mature and die**. A budding and growing leaf is dependent on ready-made photosynthates, it becomes autotrophic only after maturing, i.e. about two thirds of its final weight.

Considering **deciduous trees, low positioned buds on the base of a crown grow first in spring**, and buds on the crown top open last. There is the **opposite process in gymnosperms**. It corresponds to the intensity of the upward pressure in roots, which is very low in conifers. Opening of buds is affected by temperature and lengthening of the daytime. In lower altitudes or on warmer slopes, woods of the same species open buds earlier than in the mountains or on northern slopes. **Temperature is most important** and is valued as a sum of effective temperatures. Lower temperature requirements can be seen with mountain ecotypes of homoxylic or scattered porose wood types. Round porose, for instance ash tree, prevent from late frost by **later bud development**.

Lifetime and time of full functional capacity of leaves depends on a species and the environment. In case of **deciduous trees** with falling leaves, leaves are functional for **one growing season**, in case of evergreen deciduous, they persist for **two or more years** (*Hedera*, *Lonicera*). **Conifers** may bear needles from **2–3 years** (*Pinus silvestris*), up to as many as **20 years** (*Pinus aristata*). In general, lifetime of foliage is shortened due to inadequate conditions that are either permanent such as compacted soil, frequent or temporary, such as a fluctuation in humidity, temperature etc. Leaves on the tree crowns margin change colour first, while basal and interior more protected leaves grow old later (even though they develop buds earlier). Maturing of leaves slow down by night light. This means that the length of a growing season (defined by the number of days with favourable temperatures from spring to autumn) within one crown may be even a month longer in the crown interior.

The autumn change in colour of leaves is related to the **disintegration of chlorophyll** and covering of chlorophyll by **carotenoids** (yellow or orange leaves) and **antocyanins** (purple leaves, such as *Parthenocissus inserta*). Changing of colour is a **genetically controlled** process during which the intensity of **respiration rises**, energy rich substances, but also **mobile nutrients** such as phosphor or potassium **withdraw from leaves to storage tissues** of stems, branches or roots. This process mainly takes place at cold nights when day gets shorter; as it requires sufficient humidity. The period of colour changes lasts about two or three weeks. At the beginning of winter, leaves of deciduous trees fall off. This is how a tree gets rid of

waste matter of old, non-functional leaves. The process is controlled by growth inhibitors and can be active due to a layer of parenchyma tissue of a leafstalk base, whose solidity is violated by slimming of intracellular material, or its freezing, tearing or dying off. After tracheids are torn, a **leaf falls** off. When a leaf is off, a **new wound may be either covered by a protective cork layer**. The **fallen foliage protects the soil** from drying, enables the nutrition to soil organisms, and it generally gives organic and mineral materials back into the soil.

Though, needles of some conifers and leaves of some greenhorns (*Hedera helix*) **change colour** in autumn, as well, **without a follow up fall off**. Their colour is affected by **the change in light intensity, day length and lowering temperature**. **Needles** of spruce and pine damaged by winter drought are **redish**, their fall off is delayed. **Insufficient** nitrogen, magnesium, iron etc. **nutrition** leads to yellowing of leaves and may be caused by the lack of nutrients in the soil or limited root activity. We can sometimes see that a part of a tree foliage is green and another part is yellowish. This may mean that conductive pathways of a branch may be mechanically (e.g. by breaking) or biotically (e.g. fungi infection) damaged. Leaves on such a branch have a worsened nutrition and water balance. Brownish colour of leaves may be caused by the replacement of the central atom of chlorophyll (e.g. magnesium) by an atom of hydrogen (in acid conditions, i.e. if vacuoles are damaged, due to foliage decomposition or due to acid rain). If there is a **critical lack of water**, trees plan to decrease transpiration area by premature fall off of leaves.

6.3 The arrangement of leaves on a stem

A spot where a leaf touches the stem (as part of the node) is called a **leaf insertion**; and after a leaf falls off, this spot is called a **leaf scar**. In the leaf scar, you can observe leaf tracks (spots after vascular bundles) and sometimes even pillows. The shape and size of a scar and track character varied largely and become characteristics for discerning woody species in the winter period. Regarding the position on the stem, there are single leaves in a spiral (alternate), or pairs of leaves on one node – opposite or whorled.

Shaded branches could have an alternate distribution of leaves transforms into horizontally placed branches that are secondarily distichal, organized in one plane (*Tilia, Fagus, Picea*). We could distinguish leaves by the angle between leaves and a stem as upright (angle less than 45° degrees) and protruding (45° to 90° degrees).

The **opposite position of leaf pairs** facing each other may be cross, i.e. in two vertical mutually **orthogonal planes** (often on upright branches). Even opposite leaves may change into distichal. More than two leaves may grow from one node, such as in *Catalpa*.

A leaf occurs in a plant in **five categories**: **cotyledon** in embryo, **primary leaves** in a juvenile stage of a plant development (sometimes with shapes deviated from typical trophophylls) and **assimilation leaves** (**Fig. 24 and 25**). In the flower part, there are **upper bracts** (bracteoles) and **flower phylloms**. On the basis of a shoot, there are **cataphylls** presenting a shift from bud bracts to assimilation leaves of a growing shoot. They may be scaly, tiny, their axel buds are small, undeveloped; they grow as spare primordia and they develop branch collar in old branches.



Fig. 24 Germinated beech seedlings plotted above the soil surface cotyledon leaves (epigeic germination) which become green (chloroplast development) and start assimilation.

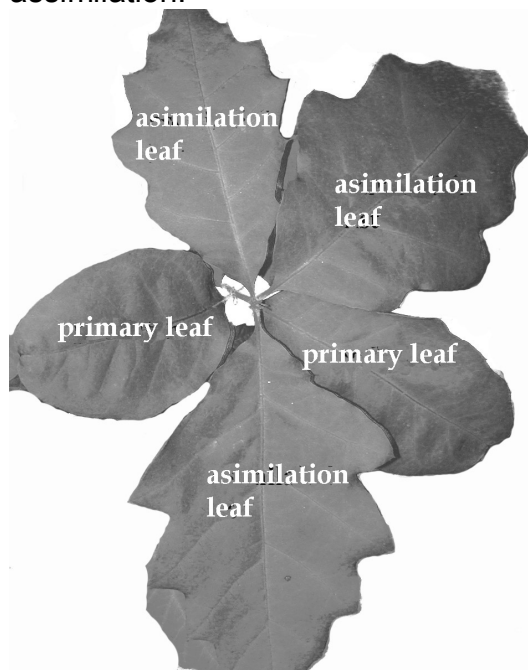


Fig. 25 Germinated oak seedlings plotted above the soil surface leaves (hypogeic germination). Cotyledon leaves lie on the soil surface a support root and stem growth.

6.4 The outer structure of assimilation leaves

Assimilation leaves of gymnospermous woods are made of a **blade** (lamina), a **petiole** and a **sheath**. Any of these parts may be absent or become stunted and their roles may be taken over by stem (*Sarothamnus*). A blade is a flattened part of a leaf. It is usually green, but sometimes can be stained with green, yellow or white spots. Some leaves can be red due to antocyanins. Some decorative conifers have a delayed generation of chlorophylls – and the light colour of young needles contrasts older green ones (e.g. *Picea abies* 'Argenteospicata').

A blade bears typical characteristics of the species (shape of the outline, edge and base, type of outline, trichomes, venation etc.) A simple blade is either undivided or subdivided by lobes of various depths. They are arranged in various patterns:

pinnately or palmately (lobed into 1/3, 1/2, or 2/3, almost reaching the main vein or blade base). If a **blade** is completely **divided into individual leaves**, the leaf is compound – **pinnate** (odd-pinnate, even-pinnate, brake-pinnate, multi-pinnate etc.) or **palmate** (tripalmate or multipalmate). In pinnately compound leaves, the main spindle (or side spindles) is held by yokes of leaves (leaves facing opposite).

The rate between the perimeter and area of a leaf blade is often higher in **xerophytes** than in sciophytes or hygrophytes (it is related to the resistance of the bordering layer of air above a leaf that prevents from an excessive loss of water). The **tolerance of leaves to solar radiation and dryness** is related to the consistence of a leaf blade and its reduction. **Sclerophylls** are solid, hard, tough and resilient leaves. **Soft blades** (malacophyllas) reduce their resilience by trichomes, **succulent leaves** increase their volume (water storage tissue).

Leaf blades are **mainly symmetric**; however, in some woods (*Ulmus*, *Fagus*, *Morus*) there is a **certain asymmetry** grounded as early as in the bud. For instance, in horizontal branches of elm, the inner half of a leaf towards the branch apex is larger than the outer half, a blade extends at the bottom near the main vein. An opposite asymmetry is typical for beech – the largest is the outer side of a leaf. The leaf heterogeneity means various behaviour and features not only of its right and left halves, but also their marginal, central, apical and basal sections.

Shaded, horizontally arranged branches have a **leaf mosaic (Fig. 26)**. This means **heterophylly**, different length and angle of petioles along with various sizes of leaf blades. This ideally utilizes the area and the leaves may optimally use the diffusion radiation. There is also a special case of **heterophylly** when a plant has differently formed assimilation leaves (**Fig. 27**). An individual plant bears leaves of the same category of different shapes (e.g. lobate pinnate sterile leaves and compound leaves bearing flower shoots *Hedera helix*).

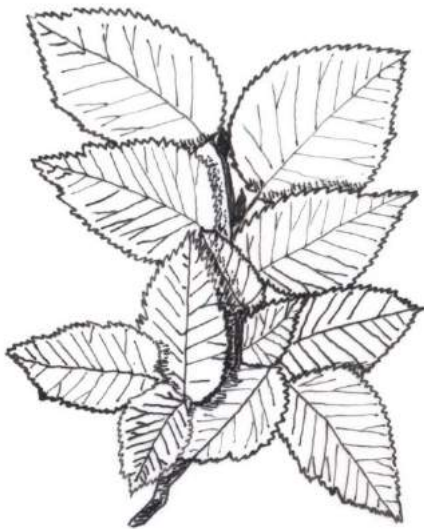


Fig. 26 Leaf mosaic develops under low light condition by leaf blade and petiole length changes. This arrangement enables maximal light capture.

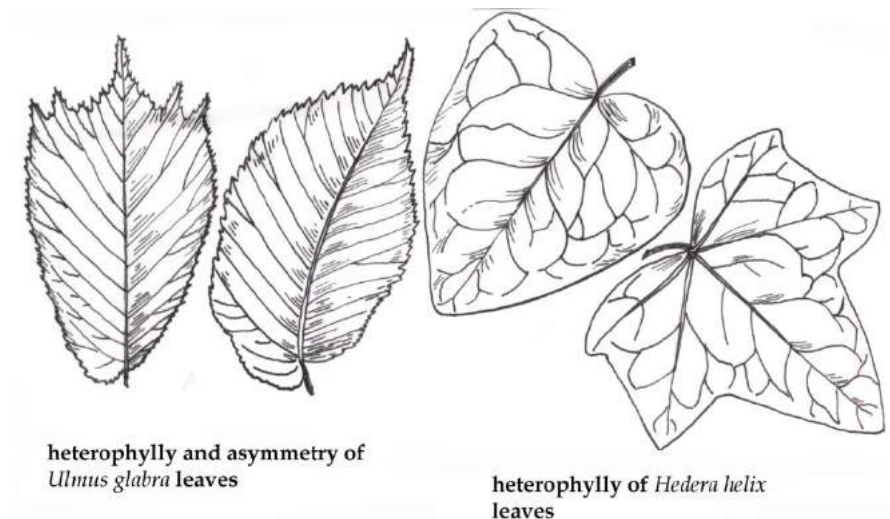


Fig. 27 Heterophylly means that different leaf shapes could be found on the one individual.

A sheath is formed by an excessive development of a base part of a leaf and is typical for monocotyledons – e.g. dracenaes, banana tree, calla etc. Leaf sheath grows around the stem above a node as high as another node, so the stem is sometimes hidden. Leaf sheaths may take part in the mechanical stability of false trunks.

A petiole is a stem part of a leaf that connects a leaf with a stem. Actually, it originates in a bud, but its growth is delayed compared to a blade development. Lower leaves of the upright shoots often have longer petioles than the upper leaves (*Acer*). **A petiole may turn leaf towards the optimal radiation** (in case of needles, e.g. spruce, they are repositioned in a bud in a spindle, into the open position of a crown top or distichal in shade); the length and angle of petioles are also utilized in the formation of a leaf mosaic. **Flattened petioles** increase leaf mobility, which also helps increase water evaporation (*Populus tremula*). Sometimes, the **petiole extends in a hood preventing a bud** during its development (*Platanus*). A leaf with a well developed petiole is called a **petiolated leaf**, a leaf without a petiole is called **sessile leaves**. We can further distinguish the following means of a leaf attachment to a stem: **sessile**, **claspig**, **connate** (the bases of two opposite leaves are joined), **sheathing** (lobes are joined around the stem). If a blade is lacking, the stalk may expand to **phyllodium** (*Acacia*, *Mimosa*). **Stipules** often replace a sheath on both sides of a stalk. They are flat, scaly or leafy, either attached to the stalk only on its base or grown up together on both sides. Stipules (membrane, scaly) protect (leaf or flower) buds and soon fall off or change into thorns occasionally (see. metamorphoses).

6.5 The inner leaf structure

The leaf is covered by the **epidermis with a cuticle**, **stomata** placed on the bottom of a leaf (in **hypostomatic** leaves – in majority of local European deciduous leaves) or on both leaf sides (**amphistomatic** leaves– *Salix alba*, *Syringa*). The **leaf surface** may be **smooth** (matte, shiny, depending on the wax cuticle structure), **wavy**, **concave**, with frequent **trichomes**. The epidermis is usually formed by a single layer of cells. If multilayer (in sunny needles), then deeper cells are called the

hypodermis. The inner space of a leaf is filled with the primary tissue **mesophyll**. There is a network of **vascular bundles** with colenchymatic or sclerenchymatic sheath, i.e. **venation** (conductive and supporting system). Sheaths of vascular bundles in woody plants leaves (except for e.g. hydrangea with isobaric leaves) reach both the lower and upper epidermis. They are divided into more or less independent alveolas (spaces), known as **heterobarical (Fig. 28)**. In case of an injury (e.g. insect sting or bite), the affected group of alveolas dies and the surrounding ones remain functional because the pressure changes do not reach them.

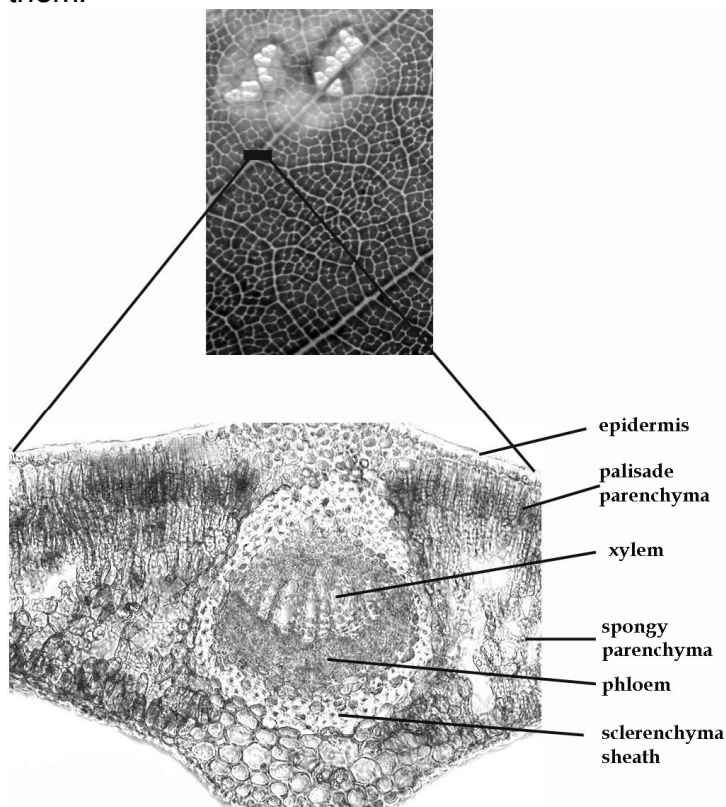
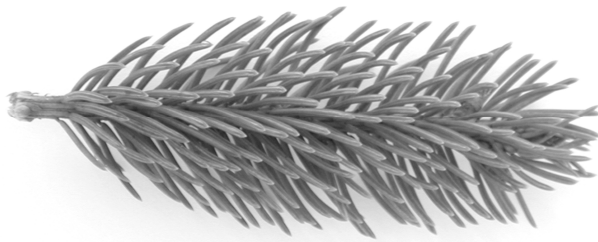
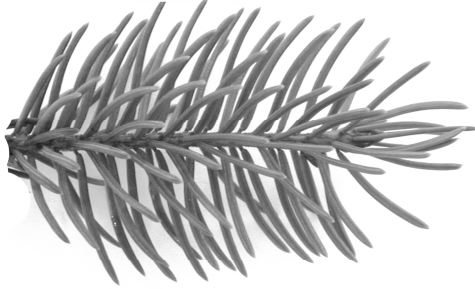


Fig. 28 Example of heterobarical leaf. Upper panel – Leaf damage is visible only in the few alveolas and neighbouring alveolas are only partly damaged. Lower panel – cross-section through middle vein – sclerenchyma sheath which connects upper and lower epidermis is visible.

Leaves are protected from insulation damage by **turning their edges towards the sunlight** (*Fagus*). A similar reaction is observable with chloroplasts in individual cells – cytoskeleton helps them get positioned so that they could take in as much solar radiation as possible in the weak sunlight, and as little radiation as possible in the direct light. According to the degree of tolerance to density of radiation, leaves in tree tops are classified into **sun or shade type (Fig. 29)**, differing by the width of cuticle, epidermis, number of mesophyll layers, density of stomata, trichomes etc. (sun leaf has a thicker skin, cuticle, thick and multilayer palisade parenchyma, a higher density of stomata, a little volume of intercellulars and a higher density of venation; generally, higher weight of dry matter related to a unit of leaf area). **The position of a leaf in space defines its water saturation** – if deficient, they fade, or even die in a green state.



sun shoot



shade shoot

Fig. 29 Example of sun shoot with dense needle organization and thicker needles (upper panel) and shade shoot with spare needle organization

Mesophyll is a basic leaf tissue derived from the stem primary bark. It fulfils the assimilation – photosynthetic function (chlorenchym). In **bifacial** leaves it is divided into **palisade and spongy layers of parenchyma (Fig. 28 and 30)**. On other hand, this distinction is less obvious in the **monofacial** leaves, similarly as in the case of needles of angiosperms (whose mesophyll makes shoulder cells – spruce, pine. In yew and fir needles, mesophyll is divided into the palisade and spongy parenchyma, and darker upper and lighter lower sides are well visible. Plants with **C₄ photosynthesis** have a **parenchyma sheath around vascular bundles** (coronary type). What is important for the exchange of gases is segmentation of mesophyll – size of intercellulars 25–50 % of the total leaf volume and the surface area of mesophyll cells (i.e. inner surface that may exceed 10–20 times the outer surface of a leaf – it serves for speeded gas diffusion and solution of gases in water film of cell walls).

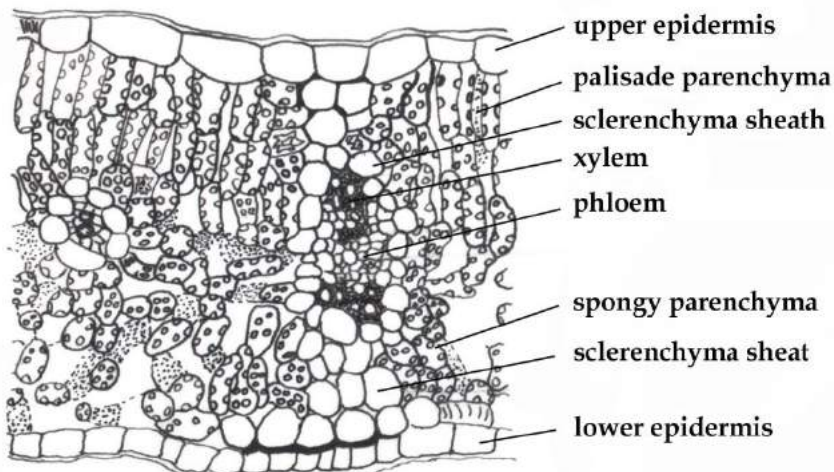


Fig. 30 Inner structure of bifacial leaf – consist of palisade and spongy parenchyma

A cuticle is a layer produced by epidermis walls on the outside of above ground structures – leaves and stems. It is made of wax. These are esters of higher monocarboxyl acids and higher aliphatic alcohols, usually in compound with paraffines, alcohols, etc. The cuticle **prevents from drying**, but also from an exchange of oxygen and carbon dioxide. It is typically structured (into trichytes, lathes, grains, moulds etc.), however, urban atmosphere, polluted by exhaust gases, aggressive aerosoles and emissions lead to its damage. **At the end of a leaf life, it is discontinuous and crackly**, which may make cuticle transpiration exceed stomata transpiration. **The rate of dying of leaves is enhanced by water stress.**

A stoma consists of two guard kidney-shaped cells with an intercellular space in between; outer walls of both cells are fixed to the surrounding epidermis cells. The openness of the stoma **can be regulated**. While surrounding epidermis cells do not contain chloroplasts, the guard stoma cells contain them. **Due to the photosynthesis, assimilation of saccharides and potassium ions**, stomata can control water accumulation, which helps them change the volume. The utilized size of a cell wall makes them long if they are saturated with water, which opens the stoma. On the contrary, if there is a lack of water, cells weaken, get shorter and the stoma shuts. Stomata are typical for the leaf epidermis, but they also exists in the epidermis of stalks and young stems. **Open stomata supply** chlorenchym photosynthesis **with carbon dioxide** and cool leaves **by water vapour (transpiration)**. Moves of guard cells are driven by the temperature, light, water content in leaves and the soil, CO₂ content in intercellulars of a leaf, wind etc. The rate of gas diffusion depends on the openness, size, shape, position and density of stomata; generally, on stomata resistance. **A high stomata resistance can be observed in leaves with submerged, tiny, densely grouped (800–1000 units per mm⁻²) and quickly reacting stomata protected by waxes and trichomes.**

Hydatods, made of two guide cells with are permanently open stomata. They are located on leaf tips or on the edges of blade teeth or fringes. A tissue with numerous intercellular spaces leads to them (**epithem**). They serve for **guttation**, i.e. exclusion of excess water from leaves (*Salix, Ulmus, Sambucus*). There are also wood species that lack guttation and hydatods (*Tilia, Acer pseudoplatanus* etc.).

Trichomes are unicellular or multicellular, simple or branched outgrowths of epidermis cells of leaves and stems. The simplest, **papillae**, cause the velvet appearance of petals. They enable easy capturing of pollen on stigmas. Unicellular trichomes may function as water reservoirs, plant protection from excessive water vapour, radiation, changes in temperature etc. **Branched or multicellular trichomes** make a perfect isolation layer (*Hippophae, Viburnum lantana*). Some types are important for their **secretion activity** (secretion trichomes).

A file of vascular bundles in a blade of assimilation leaves and other leaf organs (e.g. petals) is generally called **venation**. It is sometimes more visible from the bottom of leaves, and if leaves are transparent, they can be seen against the light. The main veins in blades with **palmate venation** direct in rays from the tip of a stalk (or blade base, such as *Acer platanoides*); in **pinnate**, side veins (first class) turn from the main vein (in the long axis of a leaf) and these branch further on into veins of higher classes (*Fagus, Carpinus* etc.). In monocots, venation is parallel, rows of veins of similar width direct from the base to the tip of leaves (bamboo), it is often also pinnate, e.g. banana and palm trees. Dichotomous venation of tree ferns, or ginkgo leaves divides several times into halves on the way from the base to the tip of

a blade; it is also an open venation. Gymnosperms have veins connected with fine **anastomoses**, whose venation is closed.

6.6 The inner needle structure

The structure of needles must allow them to live a longer life and to overcome a relatively long season of low temperatures or frost in winter and, at the same time, to survive heats and droughts and to be functional in the growing season. This is why needles have a **xerophyll** structure. Needles are grounded in buds of the **previous growing season** which **affects their future number** and structure. They begin growing in early spring of the next year, (depending on nutrients and photosynthates from older years) and they attain their permanent structure in two weeks time. As they grow old, needles change into a **shade type** structure, which is reflected in the pigment fond. Their structure is really close to the structure of a stem. On the surface, there is **epidermis** (with extra cuticle made of wax layers or fine trichomes), below which is an inner layer, **hypodermis**. Shoulder-like cells of **mesophyll** are often homogenous and correspond to cells of stem primary bark; there are frequent **resin ducts**.

The boundary between the mesophyll and the central cylinder is often made of an **endodermis**. **Lying tracheids** and **protein cells** of transfusion tissue are placed below the endoderm. This tissue is in contact with the central part – collaterally arranged vascular bundles only divided by very thin phloem-xylem rays. The **xylem part is close to the upper (adaxial) side** of a needle, the **phloem part to the lower part (abaxial)**.

Procambium in needles separates more sieve cells than tracheids. The shape of the needles cross section may be affected by the number of brachyblast needles (*Pinus*), rate of radiation during needle growth (*Picea*) and the arrangement of mesophyll (*Taxus*, *Abies*, *Larix*). **Needles are sensitive to sudden changes** such as disposition to light, wind, temperature fluctuations. If trees cannot take in enough water for frost-proof modifications before winter, they suffer from water stress and photooxidation of chlorophylls. Winter and spring are not favourable for them, especially for the individuals living near roads treated with salt. Needles, and young needles in particular, could get damaged due to frost drying.

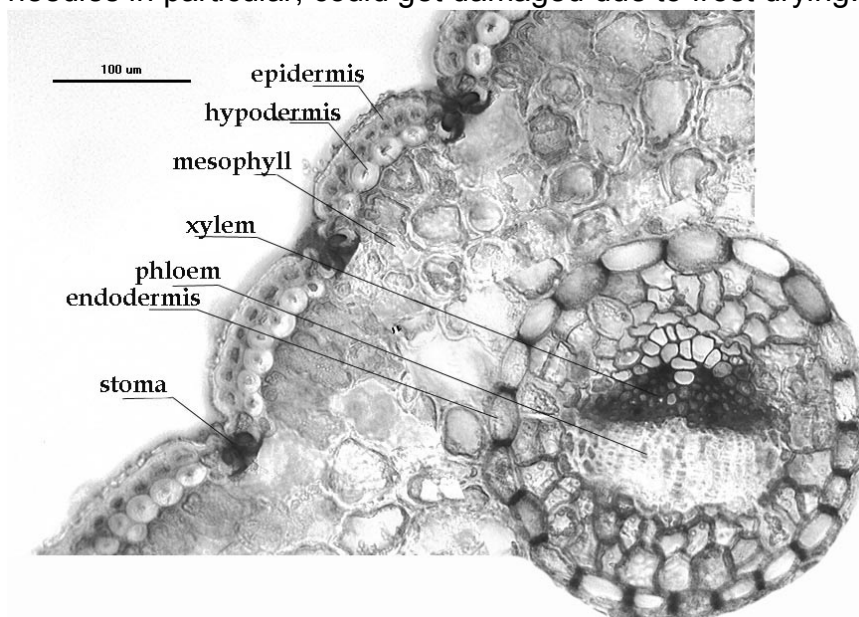


Fig. 31 Cross-section of pine needle. Stomata are nested and arranged in lines.

6.7 Evaluation of foliage state

The relation between foliage and other woody plant structures, especially heterotrophic, is a widely used diagnosis means of a woody plant prosperity. E.g. **relative weight of foliage expresses** the relation of the weight of dry leaves mass to the total dry mass. In early stages of tree life, the dry matter of leaves makes up to 50% of the total mass, and due to storing organic matter into roots, trunks and branches, this rate falls down to 5% or even below 1% in mature and old age. The **density of foliage**, utilized space of leaves in other words, expresses the volume of a tree crown space per an average leaf – which is higher in dense crowns of young trees than in less dense crowns.

The leaf area index expressed by the rate of the total cumulative area of foliage related to the area of crown projection on the ground. It can successfully express the area of reception of the solar radiation as well as the area of plant surface. This value varies from 3 to 5 in large deciduous trees (i.e. 1 sq metre of soil surface is shadowed by 3–5 sq metres of leaves), and may reach as much as threefold in case of conifers.

6.8 Leaf metamorphoses

In general, in the course of the long evolution of plants, there have been many cases of complete metamorphoses of the primary functions of leaves accompanied with changes in the structure. Cotyledons, lower and upper bracts (bractae – supporting leaves in whose axil a flower or inflorescence develop on a stalk). Other new structures include **covering scales of buds or conifer cones**, supporting scales of catkins that further lignify (*Alnus*) and covers of inflorescence (*Cornus mas*). Metamorphoses of woody plant leaves also include shoots; **spines** that have originated from the whole leaf (*Berberis*) or from stipules (*Robinia*). And, finally, **a flower** originates in the whole complex of leaves metamorphosed for the function of sexual reproduction.

7 Propagation and reproduction of woody plants

Woody species are perennial plants **anchored in the soil** by the root system. Therefore, any move from one place to another for finding a shelter is not supposable and an individual has to be able to conform to all changes on its site by its own biochemical, structural and growth activities. There are only exceptional cases when a plant could **move to another position**, e.g. due to the solifluction, landslide (mainly on slide rock), water flooding or moving of the soil by water or wind erosion, moving by snowslip, falling of banks by water abrasion etc. Nonetheless, as these plant movements are driven by exogenous factors, a plant has not got much space for the acclimatization and it is a **rare phenomenon if a plant survives**.

Yet, there exists **a movement of woody plants**, i.e. **migration**. Species spread to new sites that are more favourable to them (immigrate); they could even leave their present sites which are no more suitable (emigrate). This movement is facilitated **due to regularly produced diaspores**. Spreading of diaspores from the parent plant (**dissemination and propagation**) into various distances is defined by their shape, weight, character, number and type of activity of the spreading force. This force

includes a presence and movement of animals, direction and speed of wind, water etc. For instance, birch (*Betula*) anchenes get carried about **90 metres away**, ash (*Fraxinus excelsior*) about **2 metres**, spruce (*Picea abies*) seeds about **6 metres**.

7.1 Means of reproduction and types of diasporas

A diaspora may have a **generative origin** (changes in the genetics, i.e. by means of seeds or fruits – acorn e.g. *Quercus*, *Fagus*, berries– *Berberis* etc.), this way of spreading is called a **dissemination**. A group of individuals that originate in the genetic way is called a **generation**.

A diaspora may even be of an **asexual origin – vegetative**. This a direct continuation of a plant life via its body parts – via shoots (e.g. *Robinia pseudoacacia*, *Populus tremula*, *Rosa*), via branches that easily break off and then root (*Salix*, *Populus*) or stem or trunk stools of fallen off individuals (*Quercus*, *Tilia*, *Salix*) or via basal branches creeping on the ground that gradually root (*Picea*, *Fagus*, *Pinus mugo* and the like).

Spreading of vegetative diasporas is generally called a **propagation**. It is mainly practicable in species with high regeneration ability. The vegetative propagation of trees is can be very successful in unfavourable conditions; it diminishes the death rate of new individuals. This is thanks to the fact that the little plant remains connected to its mother plant for a longer time, and the polycormon may be more successful in the competition with the neighbouring plants. Propagation units could even settle sites with dense vegetation where seeds would have problem germinating and new sprouts would have problem developing. The vegetative reproduction is a reserve way of keeping a species on a site if conditions for the sexual reproduction (flowering) are not favourable (e.g. low temperatures in the mountainous altitudes etc.). New individuals originating in an asexual way make a **clone**.

7.1.1 Artificial vegetative reproduction

Human spreads and retains interesting cultivars, variants, hybrids etc. in both the ways – in an **autovegetative** way (cuttings, slips, layering, offsets, meristem cultures etc.) as well as in a **heterovegetative** way (grafting – suitability of a graft and a stock influencing each other must be taken into consideration).

These could be well applied to a number of cases, but always being aware of the fact that this is a rare phenomenon in the phylogenesis (long-term plant evolution on Earth). On the other hand, **vegetative reproduction is typical for the reproduction of lower organisms** (e.g. bacteria) with very short lives; **mutation and horizontal transcription of information play a vital part in the survival of a species**.

Artificial vegetative reproduction of woody plants is only reasonable in special cases and for special intentions. For instance, if we wish to sustain multiple or distant cross-breeds, mutants or other genotype valuable individuals with a weak reproduction activity, or senescent or senile individuals or if we wish to retain genetic sources and create cultivation populations (testing plantations or populations for hybridisation activities) and following populations for the mass reproduction.

Individuals in a clone may have a required united appearance and characteristics of the parent organism, but they could also gain undesirable changes, e.g. direction of growing and branching below the apex control value (especially conifers). In the adult age, the expected height might not be reached, there may be irregularities in the formation of generative organs; most frequently with monoecious species whose

flower sexuality is not controlled by heterochromosomes (e.g. grafts of fir tend not to reproduce female cones). Furthermore, they could get old sooner, their stability could be worsened due to lower wood quality and a persistence to phytofagous insects and phytopatogenous fungi. Another disadvantage in the changing environment is a lowered adaptability due to which cloned individuals need to be regularly observed and treated (e.g. limiting of suckers on drafts).

7.2 Plant life cycle and the significance of seeds in phylogenesis of plants

The plant life cycle consists of **sexual** (generative, haploid) and **asexual** (vegetative, diploid) generations. In the **phylogenesis**, there is an evident shift from completely absent changes of reproductive organs in microorganisms and rare occurrence with fungi to well developed, multiple and regular changes with an independent (algae – green, brown, red) and prevailing gametophyte (mainly in bryophytes and pteridophytes).

Seed plants have asexual **diploid sporophyte** called **zygote**. A **seed** develops from the zygote, and finally an **autonomous plant** consisting of a **root, stem, leaf**; sexual haploid **gametophyte is reduced** to a dependent part of **sporophyte** and is created only in an adult stage, i.e. after the first flowering (**male in a pollen grain, female in an ovum**). Plant life cycle enables for a **regular change of genetic information** when forming a new generation (by combining and recombining endowments) and **achieving a longer life of an individual**.

Seed plants present three wide taxonomic groups. One of the groups, **angiosperm**, have taken the greatest steps in the plant evolution – a new type of seeds developing after a **double fertilization** of an ovum (one pollen grain nucleus merges with the ovum cell nucleus to form a zygote; an embryo of a new individual develops from the zygote; the second nucleus of the pollen grain merges with the central nucleus of the embryonic cover and becomes a ground for the nutrient tissues – endosperm whose cells have a triple chromosome code). This background, which was given to a daughter generation by the parent generation, resulted in a swift entrance of gymnosperms, development of a huge number of flora species, and a quick occupation of all the continents in late Mesozoic era and in early Tertiary era.

The formation of seeds and their number is only possible in maturity, i.e. fertility of an individual, and is affected by a number of photosynthates, rate of these photosynthates transported to the generative organ and the size of seeds into which energy is transformed. **The high energetic demands of flowering**, development of fruits and seeds do not allow many tree species a regular, yearly activity, but only in **seed years** which may be of **various period** depending on a species, and endogenous and exogenous conditions. At present, when the total year temperatures sum grows, some species flower more frequently which is not suitable for them. A number of individuals (mainly in the *Picea* family) flower every two or three years. Flowering (and mainly formation of female cones) takes place in the top third of tree crowns. Needles are more exposed to the solar radiation (and temperature changes), higher transpiration (and frequent water stress) and higher demands on good working photosynthesis. The combination of stressors may result in the dying of needles (and creation of a hole) or in the limitation of elongation of growth and branching of the first class (sudden thinning of a crown). It can also be the means of growing plants in nurseries that cause changes in tree performance. A very sensitive species is larch

(*Larix*), which can flower as early as at the age of 8 years after having repetitively injured roots.

Comparisons between species prove that the number of produced seeds is often in a negative correlation with their size (a large number of very light single seed fruits of birches, on the contrary palm tree *Lodoicea seychellarum* makes a fruit with the largest seed in the plant realm weighing 1.8 to 27 kg). But in general, **seeds are very little variable**, i.e. their special and weigh characteristics vary only slightly. Moving of diasporas to new sites also depends on the distance from the source population, on barriers that may prevent diasporas from spreading (mountains, waters etc.).

The number of life diasporas, germinated seeds, varies by species and environmental conditions. The longest **lifetime and germinability** are observed in seeds of **annuals and biennials plants** (e.g. goosefoot – *Chenopodium album* – spurry – *Spergula arvensis* – up to 1600 years), while a **relative short life is seen in large seeds** of e.g. walnut (*Juglans regia*), hazelnut (*Corylus colurna*) or oak (*Quercus petraea*), a **very short lifetime is observed in willow** (*Salix caprea* only about 14 days).

The plant ability to survive in a dormant state in the form of diasporas is a result of a long plant evolution and adaptations to exogenous conditions. In immobile plants **dormation of diasporas in connection with their dissemination** is analogic to an escape of animals from unsuitable locations. The length of dormation and conditions of its interruption may be genetically defined (primary dormation) in some species and present a permanent adaptation to climatic conditions in the centre of their habitat.

A **dormation period** of seeds may be even caused by **unfavourable exogenous conditions** (secondary dormation, quiescence). When conditions improve (e.g. in species living in cleanings after coverings of the soil surface), seeds soon germinate. Not only seeds and other types of diasporas, but also **grown seedlings** may remain in some **state of quiescence** with a very limited metabolism during bad living conditions. Under an adult stand of trees and bushes or in the shadow of a building, groups of seedlings of woody plants could persist for a number of years (*Fagus*, *Quercus*, *Acer*). Slow growing due to the weak radiation, lack of soil humidity (mainly as an outcome of adult trees roots suction) keeps these groups of seedlings in a juvenile stage of the ontogenesis with a relatively low yearly mortality. These are "**candidates**" for a quick launch of growth as soon as the area gets cleared up.

7.2.1 Dissemination by diasporas of a generative type

During the sexual reproduction (i.e. creation of diasporas of generative origin, seeds, fruits etc.) genotypes are **renewed or completely new genotypes originate** during the formation of zygotes. This means that the **variability among individuals in a population increases**. A hard competitive **natural selection** comes to the scene (mainly with utilized adaptation characteristics) both in parents and young population. The natural selection, affected by accidental events, isolation etc., takes place under the pressure for the initiation and differentiation of flower organs, formation of gametes, transfer of pollen and the follow-up germination, fertilization and development of seeds and embryos, transfer of diasporas, and further on under the pressure of new conditions on germination of seeds, overcoming early and juvenile life stages of individuals in the same generation. Sexual **diasporas are located in a flower**, sometimes there are also groups of **microsporophytas** and **megasporophytas**.

A flower is a **metamorphosed shoot**, i.e. shortened stem (**peduncle**) and a file of metamorphosed leaves that participate on the sexual reproduction and spreading of seed plants (**Fig. 32**). A flower comprises of **perianth** which is divided into a **calyx/sepals** (usually green) and a **corolla/petals** (coloured) or sometimes is perianth undifferentiated (**stamens**). Sometimes a perianth may be absent (*Salix*, *Fraxinus*). **Sepals, petals and stamens** are either free or connate. Hard calyx sepals protect the inner parts of a flower, mainly in the budding stage. It usually falls off after blooming. On the inner bottom, there may be **nectaries**, e.g. in a lime. There are cases when the calyx supplements the corolla and takes the corolla colour (*Calluna*). The inner whorl, corolla, **protects reproductive organs** and attracts insects by its colour, which is mixed from dyes diluted in a cell liquid or dyes in plastides. Lower parts of its petals contain honey containers. Like the calyx, it is typically **regular** (*Tilia*) or **symmetric** (*Vicia* family). In the *Vicia* family, it comprises of an upper **pavis**, two lateral **wings** and two **bottom** leaves. **Peduncle** is typically quite small, it either expands to a sheath or sometimes may be conical (*Rubus*), convex (*Cerasus*) or extend and conves in a **cupulla** embracing a flower (*Quercus*). The scyphus or an exciple lower part of a flower, formed by the fusion of a peduncle with the lower parts of a flower whorl and filaments of stamens, which embraces a fruit completely or partly, is called a **hypanthium**.

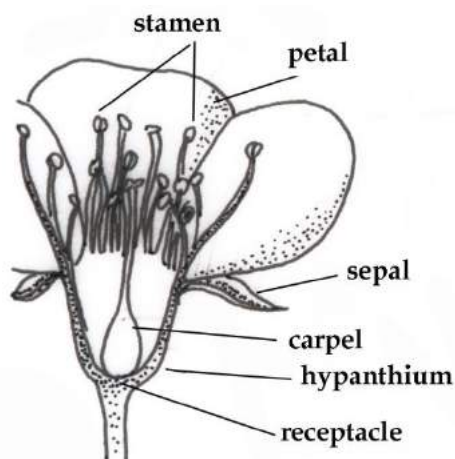


Fig. 32 Flower structure. Bottom parts of petals and sepals and stamens merge and form hypanthium. Receptacle is the modified or expanded portion of the stem that bears the organs of a single flower.

Evolutionarily older species **have spiral or spirocyclic** flowers (position of flower part in the spiral and in the circle), regular (symmetric by more planes) or bisymmetric (symmetric by two planes). Flower parts of evolutionarily younger species are arranged **in circles** (cyclical) that prone to be asymmetric (zygomorphic, symmetric by one plane or asymmetric).

The floral diagram demonstrates the scheme of a number and position of flower organs. It may be pictorial, which draws individual parts of a flower in a projection or written, which expresses the floral diagram by means of formulas. The latter is often applied in botanical encyclopaedias for determining plant species.

An inflorescence is a group of flowers arranged in a specific pattern on the common main stem (a peduncle). Leaves are metamorphosed into **bracts** (or suppressed, reduced or absent, aborted). The **main stem branches into side branches** (rachis or stalks – pedicels) of the first, second or higher classes. If the main stem remains the thickest and longest among the other branches, this type is called the **racemose**

(indeterminate) inflorescence, blooming from the bottom upward, or from the periphery to the centre – panicle, cluster, corymb, spike, spikelet, catkin, spadix, umbel, composite plant. If side branches – rachis – are longer than the main stem – peduncle, this is a **cymose (determinate) inflorescence** – blooming from the apex downwards the basis, from the centre to the edge – cyme, little bunch, rhypidium, dichasium, umbelliform, double cyme, bostryx, drepanium etc. Apex of **simple inflorescences** main and lateral branches has flowers, while **compound inflorescences** do not have flowers on the apex position. They use them to form further inflorescences. If the inflorescences comprise of the same type inflorescences, they are known as **homoeothetic**. For instance, they could be only made either of cluster or cyme subunits. If the compound subunits are different, these inflorescences are called **heterothetic**. These consist of both the cluster and cyme units. From the perspective of evolution, inflorescence is more advanced than single flowers.

Male reproductive organs are stamens, female reproductive organs are **carpels**. Flowers with both these sexes are **monoclinous** (bisexual). **Diclinous** (unisexual) are the ones that only have either male stamens or female carpels. If neither is present, these flowers are **sterile**. **Dioecious plants** have separate sexes, i.e. only male organs are formed in one individual and only female organs are formed in another (*Taxus baccata*, *Salix*, *Populus*). **Monoecious plants** form flowers or strobiles of separate sex (either male or female), but they are situated on the one individual (*Pinus*, *Populus*). **Polygamous plants** have all male, female and bisexual flowers (*Fraxinus*).

Stamens, with multiple pollen in **gymnosperms**, are arranged in a spiral into **strobili (cone)**. In **angiosperms**, **stamens are divided into a filament and an anther with four pollen sac** with a connector. They are placed on the receptacle in two or just one ring, they are altogether called **androecium**. They produce huge mass of pollen grains, mainly being of a round or elliptical shape and various sizes. A **pollen grain** is a male spore of seed plants, it generates by the reduction division in a male sporangium (anther). The pollen grains have two-layered walls – a tough outer wall called the **exine** (with a cutin, sporopollenin) and a thin inner wall called the **intine**. At pollen grain sides, there are often **air-sacs** (*Pinus*), in the *Ericaceae* family, grains are grouped in fours. A mature pollen grain (in angiosperms) contains a **vegetative cell** (tubular that disappears when pollen tubes germinate, this presents a **reduced procell**, prothallium in bryophytes and pteridophytes) and a **generative cell (reproductive, giving rise to two generative nuclei** in the pollen tube). There are also the stamens that do not create pollen, and these could be modified into scales, plates or honey containers.

Carpel, female reproductive leaves of **gymnosperms** are replaced by **seed scales**. In **angiosperms**, they consist of a stigma, style and ovary bearing ovules. The set of carpels is called **gynoecium**.

A stigma serves to capture pollen grains. It has various flaps, sculpturings and hairs. Pollen in its mucous presence germinates in **pollen tubes** which penetrate through **styles** towards an **ovule**. For instance, it takes place 2–3 weeks from the reception of pollen to the germination in beech. The **ovary** makes the lower part of a carpel. From the perspective of the position of stamens and perianth, we distinguish between a **superior ovary** (other organs below ovary), **half-inferior** (other organs around the upper part of an ovary) and **inferior ovary** (other organs above an ovary).

An **ovulum** is tied to the inner layer of **an ovary** by a funiculus that passes to the ovule base (chalaza), where **one or two integuments** develop. They surround the

inner multicellular tissue **nucellus**; with an opening on the top, which is a place (**micropyle**) for an escape of a pollen tube in the process of fertilization. During an ovule development, a **megaspore** differentiates from an inner nucellus under micropyla, and this cell gives rise (either by dividing or directly) to an **embryo sac**. After its reduction dividing, **three of its daughter cells die**, and the fourth, megametophyte, presents a haploid female sporangium – embryo sac.

A **female sporangium undergoes a multiple division** in angiosperms. This results in **two groups of four cells**; one group positioned near the micropylar and the other near the chalaza ends. One cell of each of the groups differentiate a **diploid nucleus** of embryo sac and a three-cell set remain (in micropyle an ovule set made of oosphere and two helping cells – synergids; in chalaza, a triplet of cells are antipod). **One of two generative nuclei** of a pollen grain fertilize the **ovulum** cell to form a zygote. The other one fertilizes the central nucleus of an embryo sac to form a **triploid ground for endosperm**.

A **gymnosperm ovule is simpler**. The embryo sac has a couple of **archegonia** at the micropylar end where egg channel cell develops. **Nucellus** is a place of formation of a **haploid tissue, primary endosperm**. This is formed by dividing a high number of cells prior to fertilization. Ovules are naked, easily accessible to pollen grains. The grains captured on a pollination drop released by micropylas are soaked inside as it dries down. It germinates into a short pollen tube and releases a **generative nucleus that fertilizes only the oosphere** after the entry into some of archegies.

The pollination is a transfer and transposition of pollen grains on a stigma or an ovule micropyle. Pollen is transferred from one flower to another by **insects** (entomogamous, tenomophilous species e.g. *Tilia*), by the **wind** (anemophilous, e.g. *Betula*) or by **animals** (zoophilous, e.g. cactuses) etc.

Pollination if followed by **fertilization**, i.e. the **fusion of male and female sexual cells** – gametes (male gametes are formed in a pollen tube, in which pollen grains germinate after the reception on the stigma; female gamete – an ovum is placed in an ovule) which results in the formation of a **zygote**. A zygote is a fertilized ovum cell, the first diploid cell of a new organism originated in a generative way. In seed plants, female gametes are larger. If they are immobile, they are called ovum. Male, smaller, mobile cells are called spermatozoids (bryophytes, pteridophytes). Immobile cells are called spermatocytic (in angiosperm and gymnosperms). A fertilized zygote grows into an **embryo**, and an ovum develops into a seed, and an ovary changes into a **fruit** after the fertilization.

Autogamy is a means of fertilization in which pollen is transferred onto a stigma or ovum micropyles of the same flower as the pollen. Plants practising autogamy are called self-compatible. In order to prevent from autogamy, stamens and pistils in a flower mature at different times (**dichogamy**) in both sexes of woody plants. For instance, in apples, stigmas mature first and they are fertilized from older flowers, since their anthers open after stigmas have bloomed (**proterogeny**). In lime, the principle is opposite – pistils mature after stamens have finished their fertilization (**proterandry**). Fertilization by pollen of another plant of the same species is called **allogamy**. An embryo may develop even without fertilization, by apomixis (parthenogenesis, apogamy).

A **seed** is a reproductive element of angiosperms and gymnosperms that originates from a **fertilized ovulum (Fig. 33)**. Its surface is coated by **testa** (develops from the integument) and typically includes nutrient tissues – outer (**perisperm from nucellus**) and inner (**endosperm**), sometimes only the endosperm. The testa is thin and membranous (*Juglans*), leathery (*Aesculus*) or tough (*Magnolia*). The vital part of

a seed is an **embryo** that may consume all nucellus and nearly all endosperm, while the reserve matter is placed in its **cotyledons** (*Fagaceae*) or in a **hypocotyl**. Dicots have two cotyledons, conifers have 2 to 13 cotyledons. A **hilum** may be visible on a seed. A hilum is a scar after the detachment of a different colour than the rest of the seed and with a trace of a vascular bound (*Aesculus*); a cicatrix, little scar from a micropyle opening (root base of an embryo is placed below), sometimes even a raphe. On the surface of some seeds there are various formations serving for spreading. E.g. a yew and spindle tree seeds include a **colourful arillus** made during the fertilization.

An embryo is the youngest ontogenetic stage of a plant. The very first ontogenetic stage is called pro-embryo, only containing a suspensor and an embryogene. Generally, **cotyledons, a hypocotyl, radicle and plumule** develop. A plumule is a foundation of the future stem and the first assimilation leaves. Germination, the beginning of an embryo development into a young plant, is classified by different hypocotyl growths into the above-ground (**epigeic**) and underground (**hypogeic**) germination. The hypocotyl pushes plant cotyledons above the soil surface in the epigeic germination (*Tilia, Carpinus*), while the growth of the hypocotyl in hypogeic germination is inhibited and cotyledons remain inside a seed and an epicotyl elongates (*Quercus*).

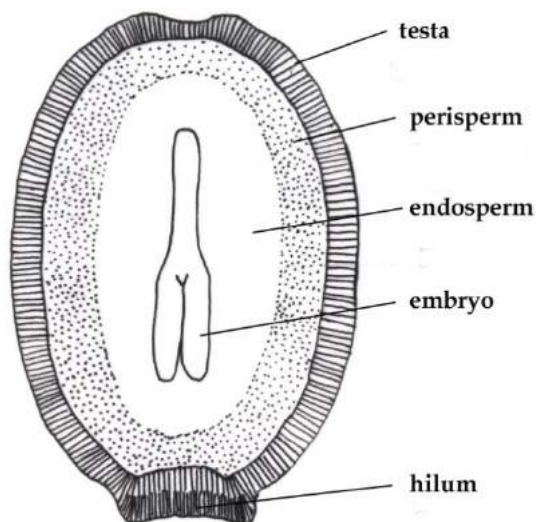


Fig. 33 Seed originates from a fertilized ovulum. In angiosperm, one generative nuclei of a pollen grain fertilizes the central nucleus of an embryo sac to form a triploid ground for endosperm. Testa envelops from the integuments.

A fruit (fructus) is a formation that **includes seeds** and was formed from **an ovary** – this is a **true fruit**. The outer ovary wall develops into a **pericarp**. It is a cover of a seed or seeds. By its position we distinguish between the outermost **exocarp** (oily skin of various colours – cherry, plum, apricot), middle layer **mesocarp** – fleshy or succulent parenchyma tissue typical for berries and stone fruits) and the inside **endocarp** – hard stone with a seed hidden inside). By the quality of **pericarp**, we classify **dry and fleshy fruits**. **Dry** ones are subdivided into **dehiscent** (vesicle, pod, silique, little silique, capsule), **in-dehiscent** (nut, drupe, achene) (**Fig. 34**). The **fleshy fruits** are subdivided into: pepo, hesperidium made of fleshy parts of the endocarp. If other flower parts participate in a fruit formation, such fruits are called **accessory fruits** (e.g. bottom parts of petals and sepals and stamens merge and

become fleshy and form **hypanthium (Fig. 35)**; a case of which is rose-hip with achene fruit, calyx becomes fleshy in mulberry etc.). False fruit is also a term for gymnosperm species – cone, compound cone, conical berry (*Juniperus*), seed berry (*Taxus*), seed drupe (*Ginkgo*). Fruits that develop without being fertilized, without seeds are called parthenocarpic.

Simple fruits originate in a single flower and their seeds are closed in one ovary.

A group of fruits from single gynoecium joint by a receptacle or another type of fusion within one flower form an **aggregate fruit** (e.g. aggregate vesicles in magnolia, aggregate drupe in blackberry). A group of free fruits is called a **multiple fruit** – *Ribes* or variously joint or fused fruits (*Fagus*, *Castanea*, *Lonicera*), originating from the whole inflorescence, i.e. is carried by a common stem.

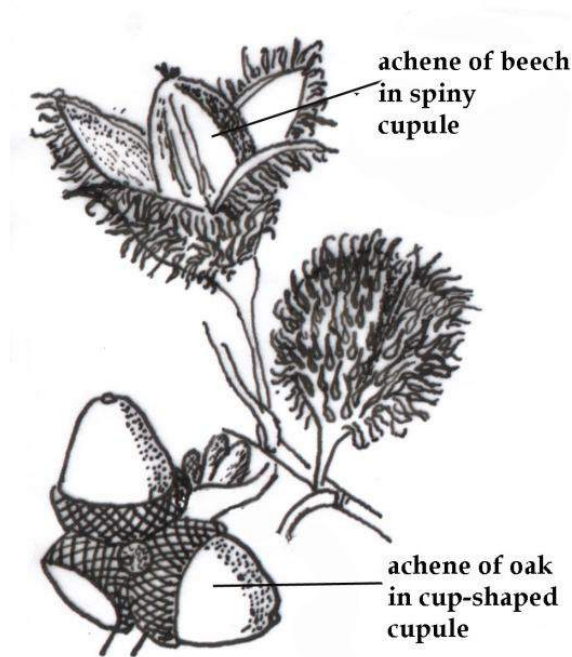


Fig. 34 Achenes (true, dry and in-dehiscent fruit) of beech and oak develop in the cupule which is of stem origin.

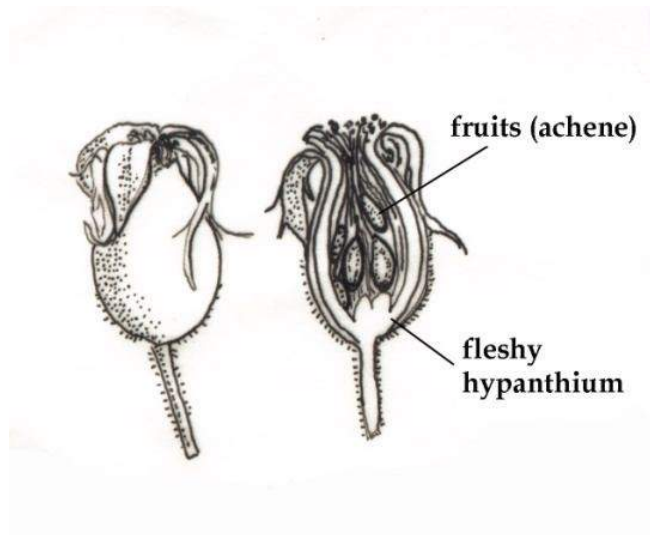


Fig. 35 False fruit of rose. Seeds (achene) were formed from an ovary after ovulum was fertilized. They are covered by hypanthium which gets mostly reddish and attracts animals to eat them – endozoochory. There are dry sepals on the top of hypanthium.

The dispersal of reproductive units of plants, such as spores, seeds, fruits, fruit groups etc. from the mother plant is called the **diaspore dispersal**. Based on the factors utilized in the dispersal, the following types are distinguished: **anemochory** – wind dispersal (*Betula*; Fig. 36); **zoochory** – via animals, this may be **exozoochory** or **epizoochory** on body surface, e.g. dry diaspores with adhesive elements, **endozoochory** – via ingestion e.g. fleshy and colourful diaspores, **synzoochory** – esp. by birds that carry diaspores on a special purpose, e.g. jay dispersal of acorns; **antropochory** – dispersal by humans purposefully or unintentionally, e.g. cultural plants, decorative plants, jagged weed); **hydrochory** – dispersal by water, rain; **barochory** – dispersal of heavier, round or oval diaspores that roll down slopes – spruce, pine cones, oak acorns); **autochory** – self-dispersal by special mechanisms including growth. The above classification is only schematic, many plant species utilize combined ways of dispersal.



Fig. 36 *Betula pendula* as an example of tree adapted to anemochory (seeds dispersal by wind)

8 Basics of woody plant physiology

Scheme of main physiological functions of above- and below-ground is given in **Fig. 37**. Water and nutrients are taken up by roots from soil and transport through sap (S) to aboveground system. Water, nutrients and CO₂ taken from atmosphere run photosynthesis in leaves together with radiation (PAR – photosynthetic active radiation). Leaf heating and wind speed up water vapour from leaves – transpiration,

but at the same time CO_2 a O_2 are received by plant. Saccharides are transported from leaves in the phloem (P) to tree apex, cambium (C), phelogen (F) and mainly to roots. All living cells respire i.e. consume saccharides a release CO_2 . Inner wood consists of heartwood without physiological function.

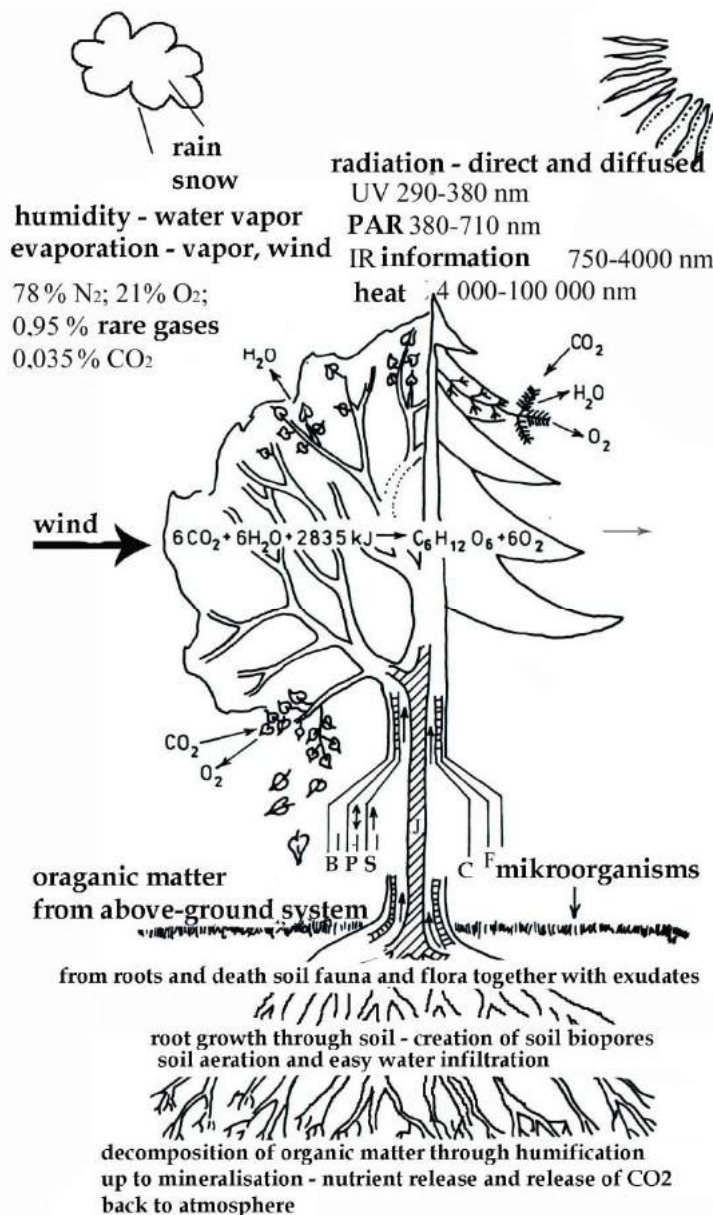


Fig. 37 Scheme of main physiological functions of above- and below-ground (according Požgaj et al. 1997)

8.1 Photosynthesis

Photosynthesis (from Greek *phos*, *photós* = light) is an **anabolic synthetic** action occurring in autotrophic, photosynthetic organisms (photosynthetic bacteria, algae and green plants), whose activity is **necessary for the existence of all other processes in life organisms**, i.e. **respiration and syntheses of all types of organic material** of the whole biosphere on Earth. Photosynthesis **facilitates the reception and binding of electromagnetic energy of solar radiation into the**

energy of chemical bonds, its utilization for breaking water molecules (photolysis), which **enriches the atmosphere with oxygen** and which facilitates **incorporation of atoms of carbon, oxygen (from atmospheric carbon dioxide) and hydrogen (from water H₂O)** into **simple saccharide molecules**. Every mol of received carbon dioxide corresponds to 477 kJ of potential energy.

By subsequent processes plants create small molecules of aminoacids, nucleotids and fatty acids incorporated in various metabolic ways into proteins, nucleic acids, polysaccharides and lipids, i.e. into the foundations of the above-molecular functional and structural systems. However, **these complex synthetic processes come after the respiration, a process characteristic for all life organisms, i.e. their living cells**. Organic substances, primarily originated in photosynthesis, function as nutrition molecules for heterotrophic organisms unable to live only from inorganic sources (herbivores, omnivores, parasites, saprophytes). In this view, all photosynthetic organisms are producers of organic matter and all other life forms – consumers, reducers (living of decomposition, mineralization of died bodies of any organisms) are dependent on them.

Photosynthesis involves **photochemical processes requiring light** (primary processes), **enzymatic processes not requiring light** (i.e. dark, secondary reactions) and **diffusion processes facilitating the exchange of carbon dioxide and oxygen**.

Solar radiation is absorbed by **photosynthetically active pigments** that occur in leaf mesophyll cells, in primary bark of petioles and stems, i.e. branches and other green parts of the above ground system:

1. **chlorophylls**: higher plants contain chlorophyll a and chlorophyll b. Chlorophylls are porphyrins, derivates or tetrapyrrole joined to complexly bound cation Mg²⁺. These are very similar to human haemoglobin in erythrocytes, but containing a ferrous atom. Their colour and function is defined by the molecular structure including the arrangement in the protein complex of chloroplast membranes (thylakoids). The content of chlorophyll a, blue-green, more active, is 2–3 times higher than the content of yellow-green chlorophyll b in shaded places, twice and more times in leaves in the sunlight. In dry matter of leaves, chlorophylls make about 0,6 % to 1,2 % depending on a species, position in the crown, development stage, radiation conditions, nutrition etc. A daily renewal of chlorophylls is 5–8 % of the total content.

Porphyrin sections of chlorophyll molecules are bound to non-polar, linear chain of phytol settling in a chloroplast membrane which secure them a special position.

2. **carotenoids**: orange carotens (α- and β-caroten) and yellow and brown xantophylls (xantophyl, zeaxanthin, violaxantin etc.). Carotenoids are isopren derivates, however, they have a linear arrangement. The alternation of double and triple bonds with delocalized free electrons is typical for them (as well as in chlorophylls).

This makes **both systems capable of receipting only a part of radiation** of a certain range of wavelength, the **remaining radiation is reflected and released back**. This reflected radiation is perceived by human eyesight as a complementary colour to the absorbed colour (e.g. leaves appear green, while they absorb blue and red range of visible spectre). **Carotenoids have light absorbing, antioxidation and ecological** (a warning signal for pollinators and animals that disperse seeds of eaten fruit) **functions**.

The first stage of the photosynthesis is the **reception of radiant energy**. To be more specific, this means the **entry of radiation influenced by spatial arrangement of branches and the foliage area in a tree crown** (or above ground system of a bush, liana and other forms), **arrangement of chlorenchyma** (tissues with cells containing chloroplasts in general), **arrangement of chloroplasts** within cells and **arrangement of pigment antenna systems**.

The core reaction centre of photosynthesis is chlorophyll a. Other colours serve as complementary colours, that, with the cooperation of enzymes and proteins form special light reception antennas – these serve for the reception of photons and control of their flow to **chlorophyll a**.

In the first stage (primary photosynthetic processes), the **solar energy is captured and stored** temporarily into the energy of chemical bonds of special small molecules of **ATP** adenosintriphosphate (in general, this molecule serves as a storage of quick energy in all life cells, even animal cells). At the same time, **energy is placed into a molecule of a reduction agent** – coenzyme nicotinamide adenine dinucleotide phosphate (**NADPH**). Both molecules are **primary products of photosynthesis** and serve as energy and reactive chemical groups transmitters. **The processes** of this stage **take place on thylakoid membranes** of chloroplasts in two interconnected steps by means of photosystems (complexes of protein molecules and hundreds of molecules of photosynthetic pigments). This is the photosystem I, evolutionarily older, existing already in photosynthesising bacteria. Then there is the photosystem II, evolutionarily younger. **Photosystem I** absorbs radiant energy of wavelengths about 700 nm (reaction centre **P-700**) receipts hydrogen for the reduction of **NADP**; **photosystem II** absorbs radiation of shorter wavelengths (reaction centre **P-680**), dissolves water molecules resulting into a molecular oxygen and hydrogen, which is used for **ATP generation**. Oxygen, as a by-product of primary processes is released into the air and is necessary for breathing of all aerobic organisms (including humans).

In the second stage (secondary photosynthetic processes), molecules from the primary processes are utilized. They **give energy** and a reduction potential – i.e. drive **the process of carbon fixation**. This **produces saccharides** out of gaseous atmospheric **carbon dioxide** (CO_2 , entering plants through stomata or lenticels) and **water** (H_2O , taken in by plant roots from the soil). This process is located in chloroplast **stroma**. It does not require light, but depends on the primary stage anyway- it finishes soon after getting dark as well.

The process of **incorporation of carbon from CO_2 into organic bonds** is defined by a plant species. In case of woody plants, there are **two types**. In the Calvin cycle, the acceptor of CO_2 is 5-carbon saccharide ribulose 1,5 biphosphate RuBP (**enzym Rubisco**), which reduces after the reception of a carbon atom into two three-carbon molecules. This way is used by **C_3 plant** species and carboxylation is catalysed by specific enzyme Rubisco. In the other cycle of **Hatch-Slack pathway**, CO_2 acceptor is a three-carbon (**phosphoenolpyruvate; PEP**), providing a 4-carbon product after the fixation of a carbon atom. This is a type of photosynthesis in **C_4 plants** where both Rubisco enzyme and PEP carboxylase enzyme participate. The final products of both synthetic ways are saccharides (photosynthates) – outcome compounds of all other substances in body and a renewed receptor CO_2 (i.e. 5 or 3 carbon acceptor – **Acc**).

In central European conditions, plants with C_3 photosynthesis prevail. They are more **sensitive to high temperatures, droughts and lack of nitrogen**. Hatch-Slack

process is present in a range of thermophyll, e.g. tropical species. Casings around vascular bundles with cells containing chloroplasts are typical for plants with the Hatch-Slack process. However, there are even such cases of plants with both types – C₃ and C₄ photosynthesis, such as corn in our climate.

Primary photosynthetic processes may be expressed by these entry factors and outcome products:

radiant energy (8 photons) + chlorophylls + 2 NADP⁺ + 2 ADP + phosphate + 2 H₂O
→
2 NADPH₂ + 2 ATP + O₂

Secondary processes utilize outcomes of the primary photosynthetic process and renew the entry factors:

$n\text{CO}_2 + n\text{Acc} + 2n \text{NADPH}_2 + 2n \text{ATP} \rightarrow \text{glucose} + 2n \text{NADP}^+ + 2n \text{ADP} + 2n \text{phosphate} + n\text{Acc} + \text{thermal energy}$

Nonetheless, **saccharide and ATP molecules** (with rich energy phosphate bond generated by photophosphorisation) are only utilized as a **source of energy for chemical bonds and a source of material** for the preparation of a range of other small organic molecules necessary for a plant cell.

8.1.1 The impact of exogenous and endogenous factors on photosynthesis

The photosynthesis outcomes are saccharides (photosynthates), basic compounds of all other material in body and a renewed acceptor of CO₂. The quality of photosynthesis in view to other life processes (respiration) is **manifested by CO₂ consumption (or release of O₂, clean photosynthesis)**. The **photosynthesis capacity** of a species (in a given stage of development and activity) means the highest speed of reception of CO₂ in a typical content of CO₂ in the atmosphere and optimal conditions of other factors (light, water, temperature, nutrients etc.). The **potential photosynthesis** is defined in the conditions of optimal CO₂ pressure. The **compensation point** (expressed by radiation, CO₂ availability, temperature...) is a state of a woody plant or its part - branch, leaves..., with a zero exchange of CO₂, i.e. balanced rate of photosynthesis (consumption of CO₂) and respiration (release of CO₂). If the conditions of the compensation point are long-term, a plant or its part weakens and dies prematurely. In shaded woody plants this often results in a limited growth, a limited immunity from pathogens and a loss of basal part of a crown (self cleaning of crown, dying of basal, extremely shaded branches). **Temperature demands** for the photosynthesis are rather lower than for respiration. The optimal temperature of central European tree species is about 25 °C. Conifer needles may have active primary photosynthetic processes even in temperatures as low as 0 °C. In temperatures below zero, the photosystem II finishes.

High portions of solar radiation (long sunny days, around the noon) may lead to the fusion of tetrapyrrol from phytol (**dephytolation** of chlorophyll), which makes chlorophyll inactive – the damaged part of a **leaf is bleached**. The **acid environment** causes a **replacement of a magnesium atom in a chlorophyll molecule** by a hydrogen atom. Moreover, this makes the chlorophyll inactive in

photosynthesis, its green colour changes into yellow-brown or brown (the affect of acid rains, browning of fallen leaves during the decomposition).

The most common reason for limitation of photosynthesis is a **lack of water**, reduced transpiration resulting in **increased leaf heating**. Besides inadequate transpiration flow, photosynthesis could be limited by **suboptimal mineral nutrition**, namely the nutrients necessary for this process – e.g. N, P, Fe, Mg, Cu, K, Mn, Cl. Moreover, a lack of water in leaves brings about a **closing of stomata** and an **increased resistance of leaf epidermis to CO₂ entry** into a leaf. If water stress lasts longer, **photosynthates are not taken away from leaves** but remain there and accumulate, which substantially **limits photosynthesis**. The speed of photosynthesis is given by the **speed of gas diffusion** (CO₂, O₂, water gases), which is driven not only by external factors, but mainly by factors such as the position of a plant as a part of a stand or as a solitary tree, the **shape and arrangement of a crown and leaves, the surface of leaves, the functions of stomata, the arrangement of mesophyll**, the system of conductive tissues etc.

Cells in green plants also contain other systems of molecules capable of utilization of solar energy. However, their activity is more complex than in chlorophylls. Such is **phytochrome** – a system of two forms of one molecule type made of a chromophore and protein parts. **P₆₆₀ and P₇₃₀ forms** blend into each other after the absorption of a photon of a corresponding wavelength and they make a **photoreceptor** of plant cells in the **red light spectrum**. Through phytochrome, light controls activity of a range of enzymes, synthesis of nucleic acids, proteins, chlorophylls and other elements, but also seed germination, flowering, leaf development and fall off, formation of buds etc.

8.1.2 CO₂ exchange in plants

The cellular metabolism of carbon is connected with the outer environment via the exchange of gases. Chloroplasts **consume** needed **CO₂ in photosynthesis**, and **release oxygen**. **At the same time**, cells constantly **absorb oxygen necessary for respiration and release CO₂**. In a given time any of the two contrary processes may dominate in photosynthesising leaves. Respiration, active in the light, consists of photorespiration and mitochondrial respiration. **During the day, the speed of CO₂ reception needed for photosynthesis related to a unit of biomass usually exceeds the speed of CO₂ release by respiration in the light**. The result is a net receipt of CO₂ by a leaf. If the rate of photosynthesis falls down, it may happen that respiration is high enough to balance it (it reaches the compensation point, see above). **If the rate of the photosynthetic activity continues to slow down, respiration prevails, and in the dark, there is only a respiration release of CO₂**.

For instance, metabolism in shaded leaves in the crown base or inner periphery or a crown core reaches the compensation point. It is a leafless space with inadequate conditions for a long-term positive balance of carbon. The compensation point may be even reached due to an increased temperature of leaves (above 35 °C), which speeds up foliage respiration and slows down photosynthesis. A range of other stressing factors including protective reactions after injuries etc may have a similar effect.

8.1.3 Photosynthesis and respiration

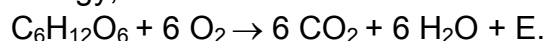
Photosynthesis and respiration are complementary processes inside plant cells, i.e. leaf mesophyll cells where **both processes happen simultaneously in separated compartments of chloroplasts and mitochondria**. On another level, these two processes within one individual plant take place in green parts (leaves, petioles, young stems etc.), while respiration only takes place in living cells with a lack of light (cells inside branches, stems, trunks, roots). This means that e.g. respiration of cells in the cambial zone also gives carbon dioxide for the photosynthesis of cells in the primary bark. At a larger scale, we may consider the relation between photosynthesis and respiration as similar to **relations between producers (green plants), reducers and consumers** (heterotrophic organisms), at first sight completely distinct from plants. This means that not all exchanges between plants and animals are one-way. Plants, animals and bacteria on Earth have coexisted for so long that **some of these organisms have become a natural part of the environment or even body of other organisms**. Some CO₂ molecules, now fixed by the photosynthesis into organic molecules of a green leaf, could be released into the atmosphere by breathing of an animal or by bacteria decomposing dead organic matter a day before. So it is clear that the utilization of **carbon makes a cycle that involves the biosphere** (all living organisms on Earth) **as a whole and extends boundaries among individual organisms**. It is similar with atoms of nitrogen, phosphor and sulphur moving between organic and inorganic realm, plants, animals, fungi and bacteria.

8.2 Respiration

Cells gain energy via the **oxidation of organic molecules**. Earth atmosphere contains a large percentage of oxygen. The bond with oxygen makes the most stable form of carbon in CO₂, and the most stable form of hydrogen in H₂O. This means that a cell is able to gain energy from **saccharides** or other organic molecules by allowing their carbon and hydrogen atoms to **bond with oxygen and the formation of CO₂ and H₂O**. Then a cell releases this energy into **macroergic bonds of ATP**. This process is called respiration and gaining energetic reserve of **oxidative phosphorylation**.

All organisms, to be specific all their living cells, respire. (Another mechanism of organic matter decomposition is a quick oxidation in burning, e.g. wood, petrol, natural gas)

The summary chemical equation of respiration is sometimes simplified and expressed as the opposite to photosynthesis, i.e. as glucose oxidation and release of energy, carbon dioxide and water:



Yet, respiration is much more complex, it processes in many controlled gradual steps and its outcome is a wide range of synthetic pathways and coordinations. That is why we recommend that respiration is studied as **a metabolic centre**. Plant respiration disintegrates complex substances with high potential energy (e.g. saccharides, fats, proteins) into simple substances and a release of energy. This **energy serves** for various cell functions – **intracellular movement, maintaining and renewal of structures, syntheses, release of heat** (e.g. in spring in opening buds and flowers). **The disintegration of respired substrate** (e.g. glucose) is a

several step process: **glycolysis, pyruvate decarboxylation, acid citric cycle, oxidation of final acceptor of electrons** (NADH₂). **Glycolysis** is localized in cytoplasm, while acid citric cycle and oxidative phosphorylation in mitochondria. The yield of the whole disintegration is 36 mols of ATP (adenosintriphosphate), 2 mols of GTP (glyceraldehyde 3 phosphate) and free enthalpy $\Delta G = -2,87$ MJ per 1 mol of glucoses. Besides the release of energy, disintegrative steps form a high number of useful products that become preconditions for photosynthesis (e.g. lignin).

Respiration is more effective in presence of oxygen (**aerobic respiration**), but it may even occur **without a molecular O₂**, by means of a chain of reduction-oxidation reactions forming simpler molecules, but still rich in energy. This is **anaerobic respiration**, further classified into **fermentation** (disintegration of saccharides and lipids) and **decomposition** (disintegration of nitrogen organic substances). Fermentation is classified by the final, accumulated and unprocessed product e.g. ethanol fermentation, milk fermentation, butter fermentation etc. These processes predominantly give energy to microorganisms (bacteria, yeast etc.).

It may happen even to woody plants that **conditions for aerobic respiration of roots are not favourable due to flooding**, compaction of soil. What is more, in decreased soil aeration, anaerobic soil bacteria produce potentially toxic compounds such as gases, organic compounds – alcohols, carbonyl group, volatile fatty acids, non-volatile acids, phenolic acids and volatile compounds of sulphur. In such a situation, even the development of tree shoots is **affected due to elongation of their internodes and limitation of formation and spatial growth of leaves, induction of leaf aging, damage and fall off**. In long term affecting, **diameter growth** of adult trees **slows down** and the structure of phloem and xylem is modified. Moreover, the **formation and growth of roots** is severely impacted, and the root diminishment is intensified by acting of r. *Phytophthora* mildews. The lowered respiration of roots results in limited photosynthesis rate since it induces the **closing of stomata** and **modifies carboxyl enzymes**, and **decreases the content of chlorophyll**. Absorbing of mineral nutrients falls with a lowered area of the root system and with a lack of energy: energy release in anaerobic respiration is weaker and does not meet the needs of root functions (ions from roots could be released into soil). Modification and reduction of root growth make **trees prone to windthrow**. The levels of auxine, ethylene and abscisic acid in stem rise, while levels of gibberellins and cytokinins fall. **Globally weakened woody plants incline to attack of biotic factors**.

Plants, or their **living cells, particularly meristems, respire continuously during the day and night, photosynthesize only in daytime (light)**. Photosynthesis prevails respiration in leaves several fold (approx. 5–10 fold). Respiration utilizes energy most efficiently from simple saccharides that cannot be accumulated in organisms in higher concentration since they are osmotically active. They typically modify into other forms or **reserve substances** – polysaccharides (most frequently starch), lipids (mainly as a reserve in seeds e.g. *Juglans*, *Fagus*, *Corylus*), and sometimes reserve proteins. **Structure elements** of cell walls in woody plants cannot be taken back as a source of energy even though they are saccharide type, such as cellulose, hemicelluloses, pectates etc.

Finally, proteins, too, make the aerobic substrate in which aminoacids as foundation stones could be reused for new or different, better functioning structures (e.g. in reconstruction of cell walls).

8.2.1 The process of respiration – oxidation of glucose

Respiration is a two step process – it begins by **anaerobic glycolysis** and continues by **aerobic disintegration of pyruvic acid or fermentation**.

8.2.1.1 Anaerobic glycolysis

It takes place **in cytoplasm** along with catalytic activity of enzymes dissolved there. It is only active **without the presence of oxygen**, even in cells located in aerobic surroundings. These two facts prove the old origin of this metabolic pathway. The **final product** is two molecules of **pyruvic acid and ATP**.

8.2.1.2 Aerobic disintegration of pyruvic acid (in mitochondria)

This process happens into these **three stages: 1) decarboxylation of pyruvic acid, 2) citric acid cycle and 3) respiratory chain (Fig. 38):**

1) decarboxylation of pyruvic acid:

One atom of carbon in the form CO_2 splits off from **pyruvic acid** (CH_3COCOOH), which means the acid is decarboxylyed, and in co-working with acetyl coenzyme A, activated **acetic acid** is formed

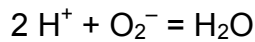
2) citric acid cycle (Krebs cycle):

It progresses in a **matrix**. The **activated acetic acid reacts with oxaloacetate, which results in the formation of citric acid**. A molecule of **ATP and hydrogen are released**. Three molecules of **coenzyme NADP^+** and one molecule of **coenzyme FAD** (flavin amide dinucleotide) reduce by accepting hydrogen and take it in the **respiration cycle**.

3) respiratory chain:

This is a sequence of **oxidation-reduction reactions**. Protons as well as electrons bring reduced coenzymes $\text{NADPH} + \text{H}^+$ and FADH_2 . At the beginning, protons get released into the neighbourhood. Electrons are transmitted by a range of transmitters into the **inner membrane of mitochondria** in the **gradient of electric potential**, and **ATP is synthesised** at the same time. ATP synthesis in the respiratory chain is called **oxidative phosphorylation**. It is very similar to phosphorylation taking place on thylakoids in photosynthesis. **Transmission of electrons generates energy** which allows for the transmission of protons via the membrane from matrix to intermembrane space to get accumulated. This is a process of foundation of mitochondrial membrane **proton gradient** (gradient pH) induced by different concentration of protons in the matrix and intermembrane space. **Protons get back into the matrix through an ATP enzyme that puts energy released during transmission into ATP**. Transmission of two protons into matrix is necessary for the synthesis of one ATP molecule. **More ATP is generated in phosphorylation** than in photosynthesis.

At the end of the chain, electrons are transmitted to the molecular oxygen. This forms **oxygen anions, that later join with protons to make water**



In oxidation processes in mitochondria, **36 molecules of ATP per one molecule of glucose** are generated.

Enzymes catalysing reactions of Krebs cycle and respiration chain are located and originate in the inner membrane of mitochondria.

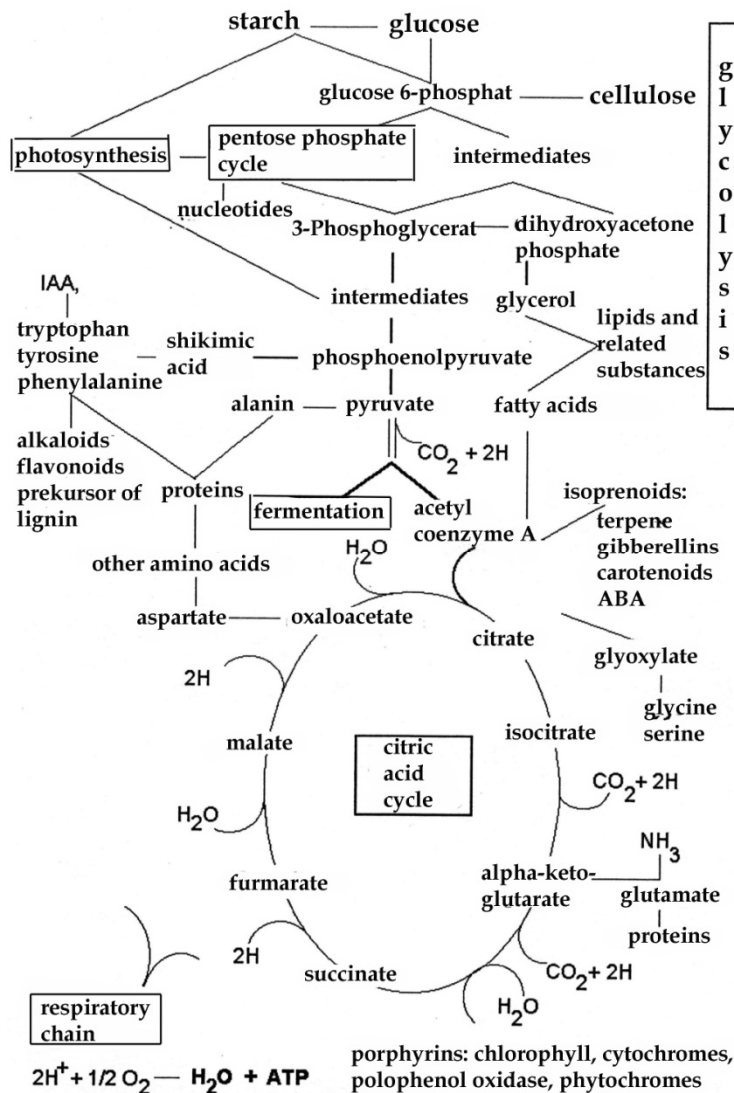


Fig. 38 Schema of main metabolic processes in plant. Products of photosynthesis are directly deposit to storage reserve (starch), cell wall (cellulose) or they entry to five carbon-sugar cycle, to nucleotides structure. Saccharides, fats and proteins can entry to process of respiration. Not only energy is produce during respiration, but also other substance are formed, which are the basis for the secondary plant metabolisms (polosaccharides, lipids, proteins, phenols, isoprenoids, hormones and many others). Thus, respiration has the key position in the plant metabolisms.

8.2.1.3 Fermentation

Pyruvic acid is degraded without the presence of oxygen and reactions stop when a semi-product is generated, e.g. ethanol. This is a case of **ethanol fermentation** occurring even in plants in anaerobic conditions (see above). **Ethanol**

is toxic, particularly **to the activities of mitochondria**; longer anaerobic conditions (mainly in summer) may lead to dying of plants. More resistant woody species include the ones that occupy meadows with regular spring flooding or the trees living in higher altitudes near mountain streams – quick and cold water is rich in oxygen. **Less energy is generated through fermentation** than through aerobic respiration as most energy is bound to final outcomes.

8.2.2 Factors of respiration

In individual plants, **flowers and unripe fruits respire faster than leaves**, roots **respire faster than stems of shoots**. The main areas of respiration in branches and trunks are in bark – mainly **phellogen, living part of phloem, cambial zone** and outer functional layers of xylem (**sapwood**) containing living cells. **Growth respiration** (breathing in growing season during growth and synthetic processes in cells) in seedlings, root and stem apices, in opening of leaves and development of fruits is from **3 to 10 times more intensive than the maintenance respiration** (e.g. winter breathing of needles). The **rate of respiration is directly proportional to the rate of growing**. As differentiation and maturation of tissues proceed, respiration activity weakens. A temporary, sharp **rise in respiration occurs during fruit ripening and leaf maturation** (i.e. climacteric respiration). This is a breakdown of substances rich in energy, withdrawal of mobile mineral nutrients (e.g. potassium, nitrogen), together with an assimilation of toxins from metabolism into a structure that is to be separated from a plant and for a preparation of the separation, i.e. healing layer. These enzymatic processes of **natural maturation** are under a strict genetic control and depend on favourable conditions of the environment. They are reflected e.g. in a gradual change of leaf colour in autumn (cells surrounding venation live longest). It is not the same as a sudden dying (e.g. due to drought), in green state and a postponed fall off. **Dying of plant cells is often accompanied with a release of gaseous metabolic products (e.g. ethylene)**.

In winter, cells in ash branches work only to survive and respiration is limited to approx. 2 mg CO₂ per hour per 100 g of fresh biomass. As soon as the growth finishes in September, respiration weakens. In woody plants, respiration increases during the secondary diameter growth and remains very active till late August, in some species even longer, e.g. oak and beech till late October, lime as late as December. Respiration in winter is balanced. It is one third to one fourth lower than in high summer. So the rate of respiration does not only alternate during the day but also during the year. **Different plant species demonstrate different rate of respiration in the same conditions**. For example, the average speed of breathing in leaves of deciduous trees is five times higher than breathing in assimilation organs of evergreens. The rate of released CO₂ and accepted oxygen (respiratory quotient) is typically one. This happens only if starch is burnt in respiration, but if fat is used (fatty seeds – *Fagus*, *Juglans*), the respiratory quotient falls below one. Yet, from the perspective of a plant sustainability, **the total yearly balance between photosynthesis and respiration is required to be positive**, i.e. photosynthesis needs to dominate over respiration. Otherwise, growth could be endangered.

The rate of respiration is affected by a number of **endogenous and exogenous factors**. The **endogenous factors** include (excluding species and individual exceptions):

1. growth

- 2. available substrate, i.e. concentration of organic compounds in cells (the higher the concentration, the higher the rate of respiration)**
- 3. amount of water in tissues.**

Seeds begin breathing more intensely as soon as they soak with water. The **exogenous factors** mainly include:

- 1. temperature:** respiration intensifies in higher temperatures (to 40 °C), and weakens in lower temperatures. Pine needles respire 25 times faster at 0 °C than at -12 °C. In the temperature range 0–40 °C, the speed of respiration grows twice to three times every plus 10 °C, but between 50 °C and 60 °C enzymes and functionally significant membrane structures are damaged by heat and respiration dies down;
- 2. light does not affect respiration;**
- 3. air humidity is a positive factor;**
- 4. a higher CO₂ concentration** in the atmosphere **slows down** respiration, 40 % concentration is harmful;
- 5. injuries** enhance respiration intensity (related to an active preparation and cell division).

As little as **1–3% concentration of oxygen** will be sufficient to a **normal progress of mitochondrial respiration**. If concentration falls below this limit, at first respiration slows down, and then the intake of water, ions and root growth decrease. Abscisic acid production rises, especially in ethylene, so the above ground growth is interrupted and leaves fall off prematurely. Inadequate conditions may launch respiration in higher plants without oxygen (**anaerobic respiration**, see above). This may happen when **roots are flooded** or when a seed germinates in the muddy soil. However, this is only an extemporaneous solution. If plants lack oxygen for longer, they die. **Plants on extremely heavy soils** with a slow movement of oxygen **develop an extensive root system** and adventitious roots. **Pneumatophores (aerating roots)** may be developed as an extreme specialisation. Plants usually use saccharides for respiration. If they happen to require some other substances, such as lipids, they modify them into saccharides by themselves. It is only an exception that a plant uses proteins for respiration.

8.3 Photorespiration

A metabolic process **similar to respiration is active in plant part which contain chlorophyll**. This process **co-works with photosynthesis, in which O₂ is used up and CO₂ is released** in the light, but, **in contrast to respiration, this is not active in the dark**. This exchange of O₂ for CO₂ is called photorespiration. It **begins in chloroplasts, moves to peroxisomes and finishes in mitochondria**. The enzyme of photorespiratory metabolism is **enzyme RuBP (Ribulose-1,5-bisphosphate carboxylase oxygenase)**. During the intake of **oxygen this enzyme splits ribulose-1,5-bisphosphate which releases CO₂**, having been taken in before. The rate between photorespiration and photosynthesis is controlled by the input of O₂ and CO₂, radiation density, temperature etc. A high partial pressure of O₂ stimulates photorespiration, while photosynthesis is stimulated by a high input of CO₂. In average conditions (21 % O₂ and 0,03 % CO₂ in the atmosphere, intensive radiation, temperatures between 20–30 °C) **plants lose about 20%, extremely up to 50 % of CO₂ gained through photosynthesis in the form of photorespiration CO₂**.

On the other hand, **this process** uses energy (**prevents from leaf overheating**) and **provides precursors** for the renewal of chlorophyll.

8.4 Water regime of woody plants

Functions of all living organisms on Earth directly depend on **characteristics of water and substances** that are either **dissolvent in water** (ions of inorganic salts, monosaccharides, proteins, organic acids etc.), or **wettable (hydrophilic), hygroscopic and soaking** (cellulose, wood, colloids), or, on the other hand, are **water repellent-hydrophobic** (fatty substances, lipids).

The most significant physical characteristics of water include:

- specific heat of ice melting (amount of energy needed for the transition of a unit of mass from solid state to liquid state) is 334 kJ.kg^{-1} ,
- specific thermal capacity (amount of energy needed for heating a unit of mass of $1 \text{ }^\circ\text{C}$) of water in liquid state is $4186 \text{ kJ.kg}^{-1}.\text{K}^{-1}$,
- specific boiling heat (amount of energy needed for the transition of a unit of mass from liquid state to gaseous state) is 2260 kJ.kg^{-1} ,

which are extremely high values in comparison to other substances. In transition from the liquid to solid state there is an increase in volume, meaning a reduction in density (i.e. ice floats on water). Water density is almost exactly 1000 kg.m^{-3} , i.e. one litre of water weights one kg.

Volume heat expansion is negligible in both the states (liquid and solid) compared to volume changes during melting or freezing. We could say that water rarely changes its volume with changing temperatures, which is true for both the stages – liquid or solid. Nonetheless, there exists a little relation to temperatures, as it is measured that the highest density of water is at the temperature of $4 \text{ }^\circ\text{C}$.

Like all liquids, water has a measurable surface tension. This is energy needed to extend a liquid surface area of 1m^2 . This value equals 0.072 J.m^{-2} (e.g. water in weightless state has a spherical shape, with the smallest area related to volume). Viscosity tells us how easily a liquid can flow. The lower the viscosity (surface tension), the weaker the resistance of a liquid e.g. flowing through a pipe (through vessels in case of woods).

The electrical conductivity of pure water in normal conditions is so low that it could be considered a great non-conductor. A negligible electrical conductivity is caused by a little amount of dissociated molecules (present in the form of hydronium ions H_3O^+ and hydroxide ions OH^-). Nonetheless, dissolution of all other elements that tend to dissociate may increase the conductivity of water solution to several fold.

A molecule of water contains two hydrogen atoms and a central oxygen atom that form an angle of 105° (in solid state – ice); this angle slightly oscillates in a liquid state. Even though the water molecule behaves neutrally, protons positioned in this angle from the oxygen atom surface cause a certain **polarity**, i.e. a weak positive charge on one side of the molecule. It results in an attraction of the positive charge side of a water molecule by a negative side of a neighbouring water or other molecule. These weak interactions appearing in a range of organic molecules (energy from 8 to 42 kJ.mol^{-1}) are called **hydrogen bonds**. In case of water, these are the factors responsible for its abnormal performance – being liquid in a range from 0 to $100 \text{ }^\circ\text{C}$, being a polar dissolvent, forming true and colloid solutions. The cohesiveness of water molecules among each other is called **cohesion**, the cohesiveness of water molecules with other molecules is called **adhesion**. Cohesion

and adhesion of water together with hydrogen bonds with a range of other structures secure compactness of plant bodies.

A constant volume and non-compressiveness of liquid water is responsible for the **diameter growth of cells** and the self-supporting capacity of unligified parts of plants (leaves, young stems etc.). Water inside cell vacuoles develops an internal pressure on the cell wall (**turgor**). In balanced pressure of vacuole and resistance from the cell wall, there is a state of fulfilled cell turgor. If cells are turgid, they develop a mutual pressure and tissues remain stable. In loss of water, they wither. There are numerous cases when cell walls in tissues are arranged in such a way that they attract molecules of water in various ways and various directions. **A change in water content leads to movements of the whole organs or their parts – e.g. change in leaf position in space and tilting, quick movements of leaves after being touched (*Mimosa*), opening and closing of pores, movements of flower sections, opening and closing of cones and changes in a position of the whole branches as a result of presence of reaction wood.**

Values of specific heat of ice melting, water boiling and specific heat capacity of water tell us a lot about the exceptional performance of **water in plant tissue thermoregulation**. Parts of woody plants with a high content of water (apices, fleshy fruits of woody species, cambial zone etc.) have a **high thermal stability**. The consumption of heat in water vapour from leaves (transpiration) is very important for **cooling** of these. On the contrary, in the process of water freezing, cooling of tissues slows down. The described water volume **changes during melting and freezing are a primary factor of damage of plant tissues**, particularly in repetitive or quick fluctuations of temperatures around 0 °C . Other water capabilities such as performing as a **reagent, donor and acceptor of electrons and as a mobile dissolvent** point out to its extraordinary significance that cannot be substituted.

Gradients in rainfall, contrast expositions and differences in texture and depth of soil, that play a vital part in water balance of plants, have an impact on vegetation, its types and functional state. Water also plays an important role in decomposition, erosion and control over nutrients in the soil. Water regime is closely tied to mineral nutrition, photosynthesis, respiration, growth and architecture of plant organs.

8.4.1 Water content and its thermodynamic state

From the perspective of phylogenetics, **life originated in water**, and water remains the primary medium of biochemical processes in plants. **Cytoplasm** contains almost **90 % of water** on average (of fresh mass weight), organelles rich in lipids as well as chloroplasts and mitochondria contain around 50 % of water, and, regarding the whole organs or tissues, **leaves and fine roots contain about 80 %**, conductive parts of xylem (**sapwood**) **about 50 %**. Above-ground parts of terrestrial **plants permanently lose water by evapotranspiration**. By the ability of plants to compensate short-time oscillation of water content and to sustain a loss of water, these types of plants are distinguished: **poikilohydric and homoiohydric**. **Poikilohydric** plants (fungi, some algae and lichens) adjust their water content to the humidity of the neighbourhood – they contain small cells without central vacuoles. **If dry**, their volume diminishes and their vital **functions are suppressed without any damage to protoplast**. Cells of **homoiohydric** plants contain a **set of vacuoles** that can balance the impact of extragenous humidity conditions to a certain extent. The development of a cuticle, trichomes, control of transpiration through pores,

suberized surfaces and ventilation systems, the development of long distance conductive systems and complex root systems securing water uptake, all of these have made **terrestrial plants capable of retaining their inner balance even in sudden changes in humidity in their neighbourhood**, and this capability has allowed for the global spread of plants. Even homoiohydric plants have stages when they perform as poikilohydric and can sustain **significant losses of water**. This concerns **ripe seeds** that retain the germination capacity for a long time, up to hundreds of years by minimisation of vital processes along with a radical limitation of hydration (water content may fall below 10 %).

Most of hydration water is bound in cytoplasm and cell wall, in the power of 1–10 (or more) MPa, depending on the density of cellulose fibres. Forces that bond water to structural elements of a matrix (cell wall, colloids) are defined as **matrix potential**. In the qualitative point of view, the significance of water contained in a cell grows with the rate of its availability. **The most accessible water is present in all vacuoles**, i.e. cell compartments specialized as water reservoirs, or in dead cells serving as hydrocytes. **Over a half of water content in leaves** is accumulated like this. Though, neither this water is completely mobile, as it is **osmotically bound** to dissolved substances such as saccharides, organic acids, secondary metabolites of plants and ions. Forces that bind water in dilutions are altogether called an **osmotic potential**. Only **purified water has the highest specific free energy, i.e. potential to perform activities (e.g. dissolve ions, cover colloid particles...) and to move freely**. Water potential of chemically pure water is a foundation for expressing a relative chemical potential of water which is tied by various forces in any place in the system of soil-plant-atmosphere. The chemically pure water potential is the **highest, meaning zero, and the potential of water bound in systems lowers, e.g. is negative**. It depends on the above mentioned osmotic potential (concentration of osmotically active substances, oligosaccharides in plant, salts in soil), pressure potential (turgor stress on cell walls from the inside of cells and hydrostatic pressure) and matrix potential (adhesion to cell walls, water cohesion of colloids etc.). **Water potential may be understood as an activity needed to develop to increase the potential of bound water up to the grade of pure water**. It is usually expressed as an amount of energy per volume unit (J per m⁻³), as a unit of energy per amount of material (J mol⁻¹) or as pressure (MPa).

The osmotic potential of a solution falls down not only with the growing number of diluted substances but also with the rising temperatures. Macromolecular substances may be present in high weight amounts without any significant decrease in osmotic potential. Though **polymerization of small molecules** to macromolecules (e.g. change of saccharide into starch and this process reversion – hydrolysis) **may highly affect osmotic potential** of a solution, which means that the net flow of water may be controlled by plant. In protoplasts with a central vacuole, there is a close relation between osmotically bound water in a cell and its availability in cytoplasm.

Water availability is expressed as a total water potential of the water system (e.g. cells, cell compartment or outer solution, usually symbolized by Ψ), which means that the more negative the water potential of a given system, the lower the water availability from the system to the neighbourhood. An osmotic component of water potential depends on the character and concentration of a dilution and is expressed by Van Hoff equation

$$\Psi_{\pi} = -\Phi R T \rho_w C = \Phi R T (N_s/V)$$

R – universal gas invariable ($8.31 \text{ mol}^{-1} \text{ K}^{-1}$)

T – absolute temperature (K)

ρ_w – water density

C = N_s/V is a sum of moles in a dilution per a unit of water weight in symplast, or water volume in a cell V

Φ – osmotic coefficient that includes non-ideal characteristics of a given dilution in the thermodynamic perspective.

Besides the osmotic constituent of water potential, the total water potential of water system contains matrix and pressure potential constituents.

A difference in potentials between places with different values of water potential (Ψ) is a situation analogical to electrical circuit with points of different voltages (U) measured in Volts. Electrical current tends to flow from a place of a higher voltage into a place of a lower voltage in the circuit. It is similar in a living plant; the current of **water flows from places of higher water potential (positive, i.e. less negative) into the places of lower water potential (more negative).**

8.4.2 The movement of water in a cell

There are two mutually interconnected water circulation systems in woody plants. **Water circulation in a cell** (small circulation) and circulation **in the whole plant** (large circulation). The small circulation secures a continual exchange of substances in a cell, and the large circulation secures transpiration and assimilation flow.

All the processes in a plant may only be realized in the state of **sufficient hydration**. **Water moves** from places of a higher water potential (average values in soil -0.1 to -0.25 MPa) into places with a lower water potential (e.g. to roots with values -0.2 to -0.3 as far as leaves with a lowered water potential -2 to -3 MPa, and then into the atmosphere with values of dozens or hundreds of MPa). Another way of balancing different gradients of water potential is a **direct movement of diluted substances** (diffusion, occurring only in the apoplast, e.g. in intercellular spaces). Though, this is **limited by semipermeability of vacuole membranes** (tonoplasts) and cytoplasm (plasmalema), that only free water molecules. The output process is **osmosis**. Water flows into a cell situated in the environment of a **higher osmotic potential (hypotonic)** from another place if a cell wall resists the pressure from the inside. If a cell wall solidity is lower, a cell bursts (**plasmoptysis**). On the other hand, in conditions of a lower osmotic potential, water flows out of the cell and protoplast limits its volume (**plasmolysis**). If a plasmolysed cell is transported into a **hypotonic** environment, it may be returned into its former state by means of **deplasmolysis**. Otherwise it dies. Plasmolytic processes are important for the diagnosis of a health state of cells and cell membranes. If they are damaged or injured, substances from its neighbourhood are free to enter the cell, and material from the inside of a cell can move out. Protoplast loses its capability of selecting passing substances.

If cells are only partially saturated with water, there is a state of **hydration deficit**. This is a cause of a water flow in a cell, or in a plant. If water deficit exceeds a certain limit, life sustaining processes in a cell weaken.

A plant needs different amounts of water in different life stages and a water potential of cells changes by this.

8.4.3 Water saturation deficit

Water saturation deficit (WSD) is an amount of water that a plant lacks to its full saturation. It is expressed in percentage and related to the maximal content of water in a plant. Variables of the original weight, weight after saturation and weight of a dry mass are studied in order to calculate the deficit.

After a little loss of water and its regaining, plants renew their natural colour and turgor of cells. Such a water deficit that will suffice for re-saturation of cells without any damage is called a **critical water deficit**. A **sublethal deficit** is such a state that projects in a plant the first damage and a **lethal deficit** is a state of a serious damage to a plant, disabling a full saturation in the future. **Water deficit has a grave impact on metabolism and physiology of cells, it slows down primary life functions of a plant and its growth.**

8.4.4 Water potential of plants

Water potential of a plant is related with other physiological processes and its annual growth. An inner constituent of water potential is **cellular water potential**; exogenous factors include **availability of physiologically present water, solar radiation, temperature** and variations of temperature and other factors.

Values of water potential of plants change during the day. **Minimal values occur in the midday or in the early afternoon.** Due to irrigation, the value of water potential of root tissues quickly rises.

8.4.4. 1 Water potential of soil

Soil humidity is the **total content of water in the soil** at a given moment and in given conditions. The **mobility of soil water and forces that tie water in the soil** are factors that influence usability of soil water by plants. The total amount of water in soil is called the **water capacity of soil**. It mainly depends on the size of soil elements. **The smaller the average size of soil elements, the larger the water capacity of soil.** A plant cannot utilize all water contained in the soil. **Water potential of soil** is the decisive factor of its usability by plants. It is a vector sum of forces that bind water in the soil. It comprises of the total water content in soil and osmotic value of soil solution.

If we take into consideration various forms of water in the soil – **hygroscopic, adhesive, capillary and gravitation water**, only **capillary water is physiologically utilizable** to plants. Differences between the absolute and biologically utilizable water content in different soils and substrates are significant for the determination of a wilting point. This point is a critical content of water in the soil below which a plant starts withering.

8.4.6 The uptake and conduct of water

8.4.6.1 Transport of water from soil to roots

Water passes into a root through rhizodermis. Then it migrates through cell walls of the primary cork to cells of xylem parenchyma. The movement of water from soil to root is realized by forces of **apoplastic movement** allowed by cell wall micellae and a colloid state of cell content. The following movement of water in a root is realized in

a **symplastic way** through cytoplasm, except from vacuoles, and through plasmodesms. The last **water movement is driven by osmotic potential among vacuoles**. Water potential falls from the surface towards the central cylinder. A sharp fall in a water potential occurs in the transition of cells of storage parenchyma through **endodermis** into a xylem conductive part. On one hand, cells soak water in, and on the other, they push it out actively.

Differences in the values of water potential in individual parts of a cell (water potential in the outer side of a cell is higher than in the inner nearer the root centre) are conditioned by the activities of a living protoplast. **Water transport is not realized only in one way, but it a complex process.**

8.4.6.2 Water conduction in a root

There are **two mechanisms** of water uptake by the root system: **active and passive**. The active uptake is characteristic for a **low release of water** by a plant, the passive intake occurs in an **intensive release of water**.

The active uptake (biological) of water by the root utilizes energy of material metabolism. The loss of water in transpiration brings about an under pressure, which leads to soaking of water in the passive uptake.

The uptake and movement of water in a plant is well described by the process of **electroosmosis**, meaning the movement of a dispergent phase (water) in an electric field towards an electrode with the opposite charge. The electroosmosis is only active if a **disperged phase is immobile, and if only the disperging environment is mobile**. In plant cells, elements of the surface layer of immobile protoplast are either positively or negatively charged, which means that a water solution moves towards the negatively charged inner surface of protoplast. The outer and inner layers of protoplast form a boundary between the water solution (as the outer environment), vacuole and cell flesh (as the inner environment), so these are media of electric charges. There is a potential difference between these two bordering surfaces. Water solution contains ions of opposite charges and hydration coat, which carry water adhering to them; the **lower the solution concentration, the more water passes into cells**. Yet, electroosmotic passing of water into cells **greatly depends on** the intensity of life processes (**respiration**) and on conditions of the exogenous environment. Due to the described processes, there are changes to the electric potential on the surface of protoplast.

8.4.6.3 Root pressure

Movement of water through a root develops a pressure that pushes water upwards into higher tissues of a plant. It is caused by forces of colloid systems and osmotic forces of protoplast or root cells. Root pressure is a physiological process requiring a **high amount of energy**. It is **active in spring** by means of an intense hydrolysis of starch into dissolvent saccharides, e.g. in tree roots. This process limits a osmotic constituent of water potential of a root structure. When the soil has **suitable humidity, soil water flows into roots due to electric gradient**, and is further pushed upwards into the above ground system. After watering, budding and development of leaves, the root pressure falls down.

Root pressure may be demonstrated during plant injuries in spring prior to budding of leaves. A liquid flows off a scar after a trauma (e.g. *Betula*, *Vitis vinifera* etc.). Besides water, this liquid contains organic substances such as saccharides, amino

acids, organic acids, enzymes, phytohormones, mineral salts etc. This "bleeding" is economically utilized for gaining organic material in many industrial branches (e.g. sugar from *Acer saccharum*). Root pressure is **highest in the morning and in the evening**, which corresponds to the values of water saturation deficit and pressure potential. Root pressure only develops a **slow movement of water** and is not able to transport large amounts of water quickly into the higher locations.

8.4.6.4 The impact of various factors on root uptake of water

Environmental factors of water uptake by plants are **direct or indirect**. Direct forces on water uptake by roots are the ones that control **transpiration** of plants (release of water). Other ones include factors that control **root growth**, since water is only taken in by young growing roots. **Soil conditions belong to indirect factors**, for example the content of water in soil, temperature and aeration of soil, water potential of soil water values etc.

The soil temperature considerably affects water absorption by roots. If lowered to 3–5 °C, the above ground parts of a plant wither even if they give out only little water. On the other hand, as soon as the temperature rises to 12–15 °C, plants return to their normal state. Thermophilic plants limit water uptake at temperatures as high as 10 °C, and they completely stop this activity at 2–4 °C. On the contrary, plants adapted to cold temperatures (e.g. ash, birch) take in water even at lower temperatures about 0 °C. The optimal temperature for intake of water is about 20 °C for the majority of woody plants. The best conditions for a fluent intake of water are when **soil temperature is 2–5 °C lower than air temperature**. This corresponds to the temperature gradient of different species. Though, cold soil is physiologically dry no matter how much water it may contain (higher altitudes). **Low temperatures affect protoplast viscosity**, which results in the changing in passing of water through the membrane system of root cells. Temperatures, too, have an impact on diffusion and other physical and chemical processes in root cells.

Soil aeration, mainly the rate of carbon dioxide and oxygen, controls water uptake by the root system. Woody plants need oxygen for respiration, growth, metabolism and the normal activity of the whole root system. A lack of oxygen limits respiration, which further affects an active uptake of water and nutrients. The **optimal content of oxygen in soil is about 10–12 %**. Too low or high content of carbon dioxide limits, sometimes even stops, the uptake of water, as well. **A rate between oxygen and carbon dioxide that does not comply with optimal plant activities occurs on compressed or flooded soils**. The water uptake can only be satisfactory if a sufficient amount of physiologically available water is present in the soil. The **optimal water uptake by plants occurs at 60–70% of maximal capillary water capacity of soil**. The most important is the soil layer with roots, making a **physiologically active profile** (vegetation layer). This depends on a species and age of an individual and on characteristics of soil layers.

Soil solutions need to have a really low concentration (0.02 to 0.05 %) in order to sustain a fluent water uptake. **Electrolytes enhance water permeability of a cell, while non-electrolytes limit it**. An experiment comparing solution concentrations demonstrated that a solution of the –0.03 MPa osmotic potential enabled plants to take in more water (up to 1.85 times more) than a solution of –0.18 MPa osmotic potential in case they could not quickly adapt to the environment. In changing concentrations of a soil solution, the water uptake more or less slows down in relation

with mineral nutrition factors. It is mainly the nitrate-nitrogen that can boost the uptake of water by roots.

8.4.6.5 Transpiration flow

Water taken up by the root system (in exceptional cases a little percentage also by the above ground structures) is conducted in various directions and to different distances into all body parts. At first, water trespasses **a root radially from rhisodermis to xylem conductive pathways**; this is a **short or medium-distance transport**. The second stage includes a **long distance transport of water via xylem elements**. In the third stage, water is transported **from conductive pathways (xylem) through leaf mesophyll to epidermis cells in leaves** till it evaporates out into the atmosphere.

Water taken up by roots sets out on a way that could be very long, often about 100 m in trees. Water can successfully overcome **long distances only via vascular bundles**. The **driving force** of the flow is a **gradient in water potentials** between two opposite apices. The flow could be broken by a **lot of resistance factors** such as **frictional force, gravitation potential etc.** Plants, especially woody species, have developed a perfect systems of tracheids, vessels or both for the conduct of water on long distances. **Water moving upwards via tracheids is filtered through pit pairs** of their tilting closings end walls. Tracheids are narrow, their conductiveness is slower than in the case of vessels. Vessels consist of individual vessels elements standing one on top of another, their cross compartments are performed to a different measure. The **weakest resistance of water conduct is developed by liana vessels**. Movement of water in deciduous woody plants is easiest in the vertical direction. It is slowest in conifers since the pathways are not vertical, but they are often spiral. Neither is it easy for water to move in the tangential direction into phloem-xylem rays that distribute water in the radial direction with a slight gradient of osmotic potential.

The highest stage of evolution is demonstrated by the conductive tissues in trees. The **youngest annual rings and young wood conduct water best, while the central wood does not conduct water at all**.

The movement of water in vessels is completely different from the movement in parenchyma cells. The current of water in vessels is directed by the rules of hydrodynamics while in living cells water moves by the rules of osmosis and overcomes the resistance of cell walls.

The most important factor in water upward movement from roots into leaves is water **cohesion and adhesion** to cell walls. Cohesion forces can lift water above barometric pressure level and reach **-30 to -35 MPa**.

Water flow from root to transpiring parenchyma: parenchyma consists of cells with a low water potential (several MPa, in woody plants -5.0 to -5.5 MPa). These cells attract water from vessels. This generates a voltage in vessels between water film molecules that move along the walls, so it appears as if all water was hanging on leaf cells. If there is a sufficient amount of water in soil and if vapour is weak, root cells support the water continuum in vessels, thus decreasing its voltage and enhancing its upward flow. **Besides water potential differences, another force of water movement is the transpiration pull (i.e. energy of solar radiation), root pressure to a certain extent (mainly in night irrigation), capillarity and changes in flow sections of conductive pathways from roots towards leaves.**

8.4.6.6 The speed of water conduct

The speed of water conduct depends on a species, ontogenetic stage, on exterior conditions, growing season (faster in spring). If physiological functions are in a healthy state, the water movement in a plant is a continuous transpiration flow. **The speed of transpiration flow is expressed by an amount of water transported via a certain part of conductive tissues in a unit of time and its fourth power depends on the area of a cross section of a conductive pathway.** In lower non-vascular plants water only spreads by means of diffusion which reasons relatively small growth of these plants. Water flow in vascular plants is faster. **If the transpiration flow is maximal, the average speed of water flow through xylem of evergreen conifers is 1.2 m per hour⁻¹, in deciduous scattered porose species such as birch or lime it varies from 1 to 10 m per hour⁻¹, and in an instance of oak this range is between 4–44 m per hour⁻¹ (circular porose species), and up to 150 m per hour⁻¹ in lianas.**

8.4.7 Release of water by plants

Especially leaves, but also stems (mainly young ones) may be studied as bodies saturated with water or **humid areas** that continuously **release water in the form of vapour into the air**. The process of water evaporation from the surface of leaves and other parts of plants into the atmosphere is called **transpiration**. It is driven by physical rules of vapour and a physiological state of transpiring tissues. Plants leaves can also **release water in a liquid state** by the process of **guttation**.

8.4.7.1 Guttation

A lot of plants are able to exclude **water in a liquid state**. This way of water release is known as guttation (from Lat. gutta – drop). A plant presses water through special pores – **hydathodes**. The cavity is filled in with thin-walled parenchyma cells, i.e. epithem that encloses a vascular bundle bringing water. The **root pressure** is a co-factor in guttation.

Guttation is not as frequent in woody plants as in herbs. It occurs when the air is supersaturated with vapour, e.g. after a warm night or in early spring in the morning when root pressure rises. Guttation is not the same as dropping of saccharide solutions e.g. from lime leaves attacked by aphides.

8.4.7.2 Transpiration and its biological control

Transpiration is a loss of water from plants by means of evaporation (diffusion process). **It depends** on physical conditions of vapour (**humidity, temperature and movement of air**), **water supply, plant species and ontogenetic stage, e.g. rhythm**. The rate of transpiration (amount of water released by a defined part of a plant in a unit of time) varies within an individual (leaves in various positions, radiation, age) by kinds of plant surfaces. **Transpiration by stomata into the air is called stomatal transpiration, transpiration by cuticle is called cuticular transpiration, and a release through bark is known as peridermal, rhytidomal or lenticular transpiration (Fig. 39). Stomatal transpiration is easy to control** for a plant – closing of stomata rises a diffusion resistance of leaves up to 50 times. A cuticular transpiration in which water overcomes the resistance of epidermis cells, may reach up to 30% of the total transpiration in hygrophilous species, 3–10 % in

conifers and only 1–2 % in succulents. The peridermal transpiration (from the surfaces of suberized stems) is comparable to the cuticular transpiration, in summer it makes about 1 % of potential evaporation. The cuticular transpiration in older well developed leaves presents about 1/10–1/20 of the stomatal transpiration. The cuticular transpiration is affected by decreasing air humidity (e.g. fall of air humidity from 95 % to 50 % brings elevates the cuticular transpiration about 5–6times), rising temperatures and pollution of air that endangers wax surfaces of leaves.

Water and nutrients are brought into living photosynthesising organs by means of a transpiration flow, and it is again transpiration that cools these organs, thus protecting them from overheating.

Woody plants that grow on **dry sites** have **thicker cuticles, small numerous stomata arranged in groups, able of quick reactions.**

The rate of transpiration changes with age. It is more intense at first stages of organogenesis than in older ones. **Injuries of plants typically enhance transpiration.** Cut-off parts increase transpiration in the first minutes, yet, it later slows down as a result of closing of pores.

Stomata make epidermis a partition with numerous openings. Water transpiration through this partition is **always higher than the transpiration from an open water level**, since molecules of vapour are not squeezed perpendicularly above the surface. They form a fan, a shape supporting diffusion of the molecules into the air. A lot of woody species face an excessive transpiration by **enlarging the border layer** of air over a transpiring leaf surface and **forming trichomes** (*Quercus pubescens*).

The area of stomata in leaf present from 0.6 to 1% of the total leaf area (Fig. 39).

The rate of transpiration through stomata is affected by the size, not by their number. Opening of stomata immensely increases transpiration, but once opened, transpiration slows down (Stefan rule of diameters). It is similar with closing of stomata: rate of transpiration decrease is not linear.

There is a **daily rhythm of opening stomata** in the majority of woody plants: there are two transpiration daily highwaves with a **midday depression**. In lack of water stomata only open in the morning. The **regulation is connected with a change in turgor of stomata cells**. Stomata are hydroactive and photoactive. Water deficit affects stomata more than light. In lack of water, they even close in the light. Permanent darkness elicits their opening, high density of radiation elicits closing, as well as short-wave rays.

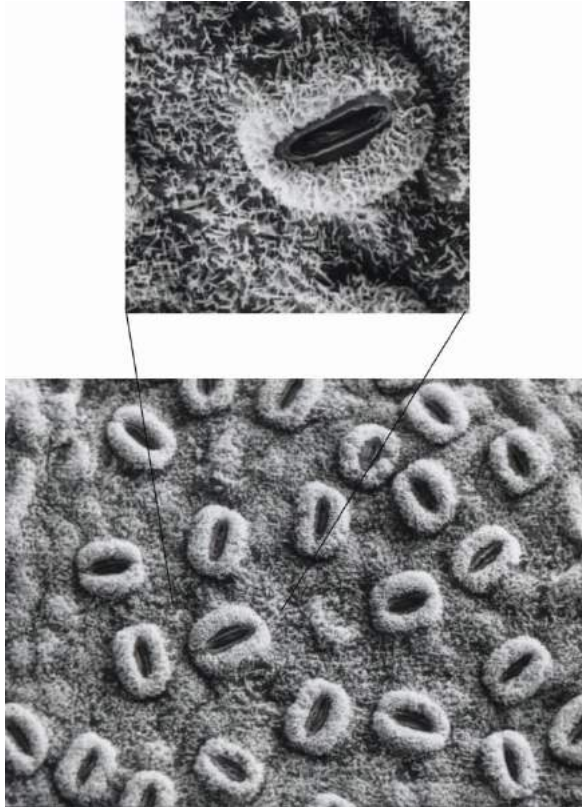


Fig. 39 Stomata on the lower epidermis of oak leaf. Two guard cells can regulate transpiration by increasing or decreasing the size of intercellular space between them. Cuticular transpiration is lower by dense cutin layer.

8.4.7.3 Environmental factors of transpiration

8.4.7.3.1 Air humidity (vapour pressure in the atmosphere)

Air surrounding a plant may contain various percentages of vapour. Even air **that appears dry contains vapour**. The absolute content of vapour is expressed either by the partial pressure or by weight units. Nonetheless, the content of vapour in the air could not exceed the level of **maximal saturation** (maximal pressure of vapour), as being **in a dynamic balance with a water level of the same temperature**. It is not usual for the **air surrounding plants to be fully saturated with vapour, which means it takes water in the phase of vapour from plants containing various percentages of water**. The movement of water molecules between a plant surface and the air around a plant is expressed as a **rate of vapour pressure on the plant surface and in the surrounding air**.

Air humidity is commonly expressed as a percentage relative air humidity (r) and is calculated from the absolute humidity (e) and full (maximal) air saturation with vapour (E), expressed in this equation:

$$r = \frac{e}{E} \cdot 100$$

The equivalent relative air humidity (r_{ek}) means a **relative air humidity, yet it does not calculate with air temperature (t_1), but a studied plant temperature (t_2)**. The **equivalent relative air humidity** is expressed in this equation:

$$r_{ek} = \frac{et_1}{et_2} \cdot 100$$

The faster the transpiration, the lower the relative air humidity and the higher the deficit of vapour. When the relative air humidity (10–20%) is very low, transpiration almost stops because of closing of stomata.

8.4.7.3.2 Temperature

A rising temperature brings about a rise in transpiration. For instance, vapour pressure in the air at the temperature of 0 °C is 4.58 mm Hg, 9.2 mm Hg at 10 °C and 31.3 mm Hg at 30 °C. If the relative air humidity is 50%, vapour pressure deficit in the above temperatures is 4.6 mm, 9.8 mm and 29.5 mm Hg, respectively. This fact reflects the progress of transpiration in the night influenced by the fall in temperatures. **Leaves**, being photosynthetic organs, **absorb solar energy** and are a location of various metabolic processes that heat them up. This results in an **increased difference between vapour pressure in the saturated environment (in a leaf) and in its colder surroundings.** In particular, plants with larger leaf surfaces (and darker colour) can rise their temperatures faster, which speeds up transpiration. At the temperature of 30 °C and the same level of radiation and relative air humidity, transpiration shall be 9 times more intensive than at the temperature of 0 °C.

8.4.7.3.3 The light

Light radiation affects transpiration both **directly by heating leaves** and other organs, and **indirectly**, as light is an **impulse for stomata to open**, which leads to a higher stomatal transpiration.

Heating due to a direct light radiation is more important to plants than a fall in vapour pressure in the atmosphere. Transpiration slows down linearly with a decreasing radiation intensity and a falling temperature. On the contrary, in case of an increased relative air humidity and decreased light intensity, transpiration rises.

8.4.7.3.4 The wind

The wind affects transpiration by **removing vapour from the border layer of the atmosphere above the leaf surface** which may increase its water deficit. The value of water potential in leaves falls due to the wind, which results in a disorder of a formation of dry matter. A permanent air move brings about a formation of xeromorph leaf structures. Plants get lignified and air holes get smaller.

8.4.7.3.5 The soil and other factors

This group of factors includes **soil composition, soil humidity and content of nutrients, air and gases in the soil.** As stated above, not all water contained in the soil is available to plants. The most suitable water capacity in the soil is 60% of the full water capacity in the soil in terms of water available to a plant.

Transpiration in more fertile soils is lower. Even artificial fertilization can decrease transpiration. After taking nutrients up, a plant changes its osmotic-colloid

characteristics of the cell content. Absorbed nutrients play a part in the control over the content of different forms of water in a plant. Nitrogen fertilization usually slows down transpiration temporarily, but the subsequent growth of the foliage area speeds transpiration up. Phosphoric acid fertilizers decrease transpiration as potassium fertilizers do. Calcium affects various plant species differently, sometimes leading to a rise, other times to a fall in transpiration.

The process of transpiration is greatly affected by the temperature of the soil solution, the content of oxygen and other gases in the soil that are secondary factors. They either slow down or speed up the uptake of water by roots, which influence transpiration secondarily.

Exogenous factors of transpiration include **emission, smoke gases and quakes**. Fly ash increase transpiration secondarily – as it falls on a leaf surface, it brings about a corrosion of the cuticle or a grave dehydration of leaf tissues, thus increasing transpiration. Quakes also bring about the increase in transpiration. This means it is necessary to transport plants with a proper care.

8.4.7.4 Quantities of transpiration

The greatest consumption of water for transpiration occurs in late spring when woody species have developed a foliage surface and the majority of leaves have matured for photosynthesis. Moreover, this is a season of the **quickest growth and longest daytime**. In central Europe, this season dates from May till late June, depending on a species.

On a sun shining day, woody plants transpire 5–10 g of water per 1 m² of foliage area per an hour. Conifers transpire only about 1/10 of this volume by deciduous trees. A beech forest (1 ha) transpires from 25.000 to 30.000 of water daily, and 3.600.000 kg of water in a growing season.

The transpiration capability (i.e. rate between the amount of transpired water by a plant and the potential evaporation – at the same place and time, or relative transpiration) and **maximal transpiration** (i.e. average maximal speed of transpiration measured at a natural site) **are necessary quantities for the estimation of water consumption by individuals of the same species at different sites**. The amount of water (e.g. in litres or tons) consumed for a plant or stand transpiration in a growing season per a weight unit of dry matter (kg, t), is called a **transpiration coefficient**, or the inverse value, i.e. **efficiency of water utilization**, known as transpiration efficiency. Water turnover is a period of the exchange of water in a plant (by means of transpiration and uptake of water). A plant uses only about 0.01–0.08% of the total amount of transpired water for the creation of a dry matter. The absolute majority of transpired water only serves as a medium for nutrients and other substances transported in a plant body and as a cooling system.

8.4.7.5 Anti-transpiration substances

A decrease in transpiration means a change in related physiological biochemical processes. **Anti-transpiration substances help decrease transpiration of 60–80%, while leaf temperature rises of several degrees**. Anti-transpiration substances also control the uptake and transport of ions.

The main reason for the application of anti-transpiration substances is to decrease transpiration at a certain period, thus **protect plants from a lack of water**. Yet, it is

not clear if **anti-transpiration preparations do not limit the entry of carbon dioxide into a leaf, which would subsequently affect the photosynthesis.**

Experience in the application of various anti-transpiration preparations shows that the application is expensive and is not as efficient in numerous cases as was expected. The anti-transpiration substances are recommended to be applied prior to transporting during transplanting in a growing season, as they improve the success of transplanting. Transpiration may be as well weakened by the increased content of carbon dioxide in the air (greenhouses) or by the application of some growth inhibition preparates (abscisic acid etc.).

8.4.8 Water balance in a plant

We distinguish between an **active and a passive water balance.** The **active** (positive) water balance is a state when a woody plant plays an **active part in water saturation.** The **passive** (negative) water balance means an **increase in the water saturation deficit and a disorder in water management.**

The **optimal water balance** is a state when a plant does **not suffer either from a lack or a surplus of water,** meaning that the activity of roots, rate of flow and transpiration are maximal. As soon as the balance in the receipt, conduct and release of water by a plant is disturbed, a greater water deficit brings about withering, related with the accumulation of abscisic acid and a decrease in the content of gibberellins in leaves. There are the **following stages of withering: beginning, temporary, permanent, irreversible.**

The beginning stage of withering occurs to woody plants in hot summer days when roots do not have enough capacity to store above ground parts with such a high amount of water that is transpired due to high temperatures of the air.

Another problems may include the **elimination of conductive pathways due to entry of air from neighbouring tissues (formation of air bubbles and embolisms), or blocking of conductive pathways by the growings from surrounding parenchyma cells, thyllas.** Especially round porose woody species incline to thyllas and embolizations. Conductive pathways of woody species may be made **dysfunctional also by parasitic fungi or damaged by phytofagous insects.**

In the night, there is a decrease in air temperatures and a lack of available water in soil, so a plant replaces the lost water, in the morning it is saturated with water and appears fresh – turgescient. **A greater water deficit in a plant results in a fall in carbon dioxide uptake and limitation of photosynthesis due to closing of stomata.** In lack of available water in the soil or in hypoxia (lack of oxygen due to compression of flooding) or salting, the beginning temporary withering usually passes into permanent irreversible changes, which brings about a deep and permanent damage that is reflected by **accumulation of toxically substances, changes in growth and gradual dying.**

8.5 Mineral nutrition of woody plants and the significance of nutrients

Plant nutrition, i.e. substances gained from the neighbourhood and assimilated substances in the body, is mineral in autotrophic species, organic in heterotrophic and both mineral and organic in mixotrophic species. The nutrition is received by body surfaces, which are really extensive in plant bodies compared to their volume.

In woody dry matter (with no water), there is approximately **45% of carbon, 42% of oxygen, 6.5% of hydrogen and 1.5% of nitrogen.** Carbon is taken in the form of

gaseous CO₂ from the atmosphere (besides a negligible amount in a liquid stage taken up by roots from soil solution), oxygen originates from CO₂ and hydroxyl ion (OH⁻), hydrogen is from water molecules (H₂O) and nitrogen along with the remaining 5% of mineral substances from the soil.

Individual elements in a **fresh weight of plants** are represented in the following rates: **P, K, Ca, Si, S, Mg, Fe, Na, Cl, Al** in 10⁻¹ to 10⁻²%, known as **macroelements**; **Mn, B, Sr, Cu, Ti, Zn, Li, Ba, Br** in 10⁻³ to 10⁻⁴%, i.e. **microelements** and traces **As, Mo, Co, I, Ge, Pt** etc in 10⁻⁵, **ultramicroelements**.

Ash elements are inorganic – **mineral elements** that remain from the dry matter of a plant body after burning. **Burning releases carbon and nitrogen from organic bonds**, both of them in the form of oxides. Most ashes are included in bark and leaves (3–8% of dry matter), least of them is in wood (0.4–0.5%).

The above named mineral nutrients are also classified by the rate of the necessity (physiological effect) and by the form they are absorbed – as cations, anions or heavy metals. **The ones with life significance are the nutrients without which a plant is not able to enclose its life cycle**, i.e. cannot give rise to germination seeds and a new healthy generation. Moreover, these elements are not replaceable by any others. These are **biogenous elements** with building or control functions – catalysers, cofactors, moderators. By the general significance and content, they are divided into **macrobiogenous (anions: C, O, N, P, S, cations : H, K, Ca, Mg, heavy metals : Mn, Fe, Cu, Zn) elements** and **elements in a smaller, or even trace content, called oligo-biogenous elements (B, Cl, V, Mo, Bi, Ti, Ba, Li, Co etc.)**.

Qualitative requirements for the nutrition are **more or less same in all green plants**. They **differ in quantitative requirements** that mainly reflect in different mutual rates. While imbalanced nutrition, mainly by oligo-biogenous elements hardly exists in natural conditions, human activities (by growing of single species and same age stands, improper fertilizations and irrigations, chemical preparations in winter, emissions, increase of CO₂ and NO_x in the atmosphere) violate the nutrition both by biogenous and oligo-biogenous elements.

The source of nutrition is mainly in the solid phase of soil that releases elements in the liquid phase to move to roots by diffusion or mass flow – rain water or transpiration. **Root exudates** help make them more available (hydrogen cations, acid carbon anions and organic acids). Then, individual nutrients enter roots via **diffusion, absorption exchange for excluded cations and anions and further on actively, with the assistance of macromolecular protein transmitters**. So a plant needs to give out energy (ATP) gained in respiration of root cells in order to take in nutrients into roots. This means that the **uptake of nutrients** needed to satisfy the following needs: satisfactory temperature regime, sufficient water and oxygen in soil, photosynthates in roots that become sources of energy in respiration. **Healthy nutrition of trees is also influenced by the volume of soil utilizable by roots and capabilities of an individual to form, extend and maintain a sufficient sorption area (surface of fine roots and root tips)**.

Another source of nutrients is their **recoverability – e.g. in the fall of died plant bodies (leaves, bark, roots) that are decomposed by soil organisms**, releasing mineral nutrition for a new usage. The recoverability of nutrients is also active by **secretion and excretion** of plant elements, and to a little extent also by **washing away** of easily mobile ions from leaves. Leaves that are lower positioned in a crown of a tree can receive ions washed away from leaves positioned above them. This makes a little receipt of nutrients by leaves. Leaves secure the carbon nutrition (control element of quantity of plant production), though they are able to receipt even

some ions and molecules through stomata or injured cuticle, e.g. ions of potassium, sulphates, nitrites and nitrates, saccharose (i.e. nutrition else that in roots that is successfully applied in intense agricultural fields and plantations of fruit trees as leaf fertilization, or, on the other hand, entry of toxic elements into plants through the barrier of covering tissues of a stem system).

Though, **the main role in the woody plant nutrition is played by the root system, not only in the uptake of nutrients, but also in the control of storage, mobilization and separation into the above ground system.**

8.5.1 Roles of individual nutrients

The roles of individual nutrients can be briefly described as follows: carbon, oxygen and hydrogen (C, O, H) are the building stones of saccharides, organic acids and lipids, while carbon is (almost) only accepted by leaves in the form of CO_2 and hydrogen comes from water taken in by roots.

Nitrogen (N) joins these three elements during the **synthesis of amino-acids** (some of which contain sulphur). **The uptake is active from the soil**; in pH up to 6.8 it enters root in the form of NO_3^- and its incorporation needs an active participation of nitrate reductase and hydroxylamine reductase. The intake in the form of NH_4^+ dominates from pH 7, and it may be toxic in alkaline environment (it reduces intake of cations, and even causes the release of K^+ and Na^+ from roots). The incorporation of this form into aminoacids causes a release of H^+ and may lead to a rise in acidity of the cytoplasm. This danger is serious, particularly in urban coniferous stands as a result of a high number of irresponsible dog keepers. Nitrogen may also be **absorbed in oxides** that originate in the atmosphere during electric discharges (including combustion engines) and that are **dissolved in rain water**. They could be **absorbed by leaves and roots**. A higher nitrogen nutrition launches growth, limits early maturation of wood and makes woody plants more sensitive to parasitic fungi and unstable temperatures, especially low temperatures.

Phosphor (P) is bound in **nucleoproteins and phospholipids**. It is essential in **energy needs** of metabolism (**phosphorilation of saccharides**, energy containers of **ATP, ADP** – adenosine triphosphate, adenosine diphosphate, etc.). It is receipted as H_3PO_4 or PO_4^{3-} . The **intake grows in the presence of calcium cations and borates** (synergy, see below). Phosphor transport and redistribution takes place in phloem sections of vascular bundles.

Sulphur (S) is absorbed in the form of **sulphates and stimulates the intake of nitrates**. Its way into the apoplast is passive, and it is transported into the symplast by a specific permease built in the cytoplasm membrane. It is quite soon, already in roots, that sulphur incorporates into specific proteins (**cystein and glutation**), constituents of the **antioxidation system**.

Potassium (K) enters a plant as a potassium univalent cation as an exchange for a hydrogen cation released into the rhizosphere by root cells. It can **activate about 60 enzymes** in the respiration process, utilization of energy, reduction of nitrates, protein syntheses and reserve saccharides. It plays a **significant part in the hydratation of tissues and is released from cells in stress**.

Sodium (Na) is taken by plants in less quantity than potassium, it **accumulates in vacuoles** and acts as **osmotic agent in halophytes** – plants growing in saline environment (mangrove swamps). Though, the absolute majority of woody plants

control water movement in body by means of **osmotically active saccharides** or by means of other simple organic substances (e.g. proline proteins etc.).

Calcium (Ca) participates in cell hydration by **stimulating the uptake of K^+** , **stabilizing membranes** and eliminating the permeability of these, and by eliminating the release of ions, it can also activate certain enzymes, control elongation as well as diameter growth and it takes part in the preservation of a good state of cell environs through **detoxication of organic acids**. A considerably high amount of Ca is contained by cell walls (**Ca-pectates**), while its concentration in cell cytoplasm is very low.

Magnesium (Mg) is a constituent of **middle lamellas in cell walls, of chlorophyll molecules** (as a central atom of porphyrin complex) and cooperates on the formation of granas in chloroplasts. It **activates Rubisco** (one of the most significant enzymes of photosynthesis) and **DNA-polymerase enzyme**. It is a part of some proteins, it **controls water regime and phosphate transport**.

Iron (Fe) presents a transition to oligobiogenous elements, it occurs in the **form of organic (chelate) bonds**, it is **essential for the synthesis of chlorophyll and reduction oxidation processes in metabolism**.

Boron (B) is needed for the **metabolism and transport of saccharides and phenols**, it plays a part in the **elongation of pollen tubes and root cells, and, above all, in the synthesis of nucleic acids**. Moreover, the presence of boron (in relation with the transport of phenolic substances) decides over the **accumulation of lignin** and other defence structures.

Manganese (Mn) in enzymes acts in the process of **oxidation** (namely in respiration), **nitrate reductions, control of the rate of divalent and trivalent iron** and in the processes of photosynthesis.

Copper (Cu) **stabilizes chlorophyll** (through the influence of protein synthesis of chloroplastic structures), it is a **constituent of enzymes, it affects nitrogen metabolism**. In the form of oxides and phenolases, it takes part in tissues lignification.

Molybdenum (Mb) is a constituent of **nitrate reductase**, and it supports the assimilation (**fixation**) of **nitrogen**, required by soil microorganisms.

Zinc (Zn) has a range of functions in the oxidative **metabolism and hydrolytic reactions**, it affects the **assimilation of saccharides, biosynthesis of proteins and some growth elements**.

8.5.2 Ion relations

The **ion antagonism** is a phenomenon in which **parallel factors generate opposite effects**. In case of mineral nutrition this means that **one ion eliminates the entry of another ion** into a plant. E.g. an increased concentration of K^+ and Cl^- in the neighbourhood leads to a limited uptake of Ca^{2+} , Mg^{2+} , Na^+ , but also of phosphorus and sulphur. There are more antagonistic relations between ions, such as between magnesium and calcium, phosphorus and calcium, sodium and calcium, between forms of aluminium and iron and manganese and iron.

Moreover, the principle of **synergism** is applied in the uptake of ions. This means that a **two parallel factors have greater influence than if they were affecting individually**. For instance, the increased intake of nitrogen (NH_4^+ , NO_3^-) or calcium

(Ca²⁺) stimulates the intake of potassium (K⁺). Potassium ions have a positive effect on the phosphorus intake.

On the other hand, the synergism may have a negative affecting, as well. Sulphur dioxide and nitrogen oxides, if present along with ground ozone, cause more serious damage to woody plants than if they acted individually.

Besides the ion relations, the **nutrition intake also depends on the ion form** in the soil. E.g. K⁺ from **potassium sulphate (K₂SO₄) is better accepted than K⁺ from potassium chloride (KCl)**. Nutrition changes may be also caused by the **competitiveness of ions** that is reflected in confusing a ion needed for nutrition with another one of a similar structure. Such a relation may be observed with **potassium and rubidium ions. They both share the same active binding centres** of transmitting; so some centres are blocked by rubidium and cannot take a needed amount of potassium. In another case, if significant respiration pathways are blocked by an inhibitor, root cells may lack energy for an active distribution of needed nutrients through barriers of cell membranes.

Another nutrition aspect is a **plant capability of utilization of the absorbed nutrition** (e.g. to build it in a corresponding structure, enzyme etc.), or **translocate it into places with higher demands** and reutilize one ion. On the other hand, a plant needs to be capable of **immobilizing** nutrition absorbed in a surplus amount and **detoxication** of some toxic substances (condensing of calcium ions and formation of oxalate crystals or carbon calcid, chelating of heavy metals etc.).

8.5.3 Nutrition disorders

Nutrition disorders include **not only insufficient nutrition** by some elements (differentiation), but **also surplus nutrition (luxuriant) and imbalanced nutrition**. Trees react to nutrition disorders by **changes in growth and its timing**, but if the disorders are more serious, it may lead to disease and visible damage to a plant, and these changes (e.g. colour of leaves, changes in the development of certain structures etc.) are evaluated as a deficiency disease.

For the **adequate plant nutrition** it is necessary that the intake of elements, their transport (complicated in some elements due to immobility of these) and utilization are not **disrupted**. Therefore the **standard of mineral nutrition** (e.g. availability and usability of nutrients) needs to be **studied as a whole from various angles**. This means to analyse it from the perspective of **soil conditions** and its physical chemical characteristics, and from the perspective of the **plant** which is complex since the occurrence of substances, amount of substances, form and mutual ratio of substances varies by structure, species, ontogenetic stage, season. All these factors show that even a fertilization decision which seems easy at first sight may be a contra-productive action.