Chapter 5
Structure

5.1 Hierarchy of Structure

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The scope of our considerations in the present book covers a wide area from subcellular plant parts to a global vegetation zone, in particular the boreal forest. There are, however, natural hierarchical levels in the structure which are necessary to understand in the study of natural phenomena in such a zone. The hierarchical structure we will describe here will be utilized later in our discussion in Chapters 7–10.

A central challenge in ecology and forest growth studies is to understand the emergence of ecosystem behavior from the interaction of its components. For example, a forest stand can be regarded as an assemblage consisting of living organisms, especially trees, their organs and ultimately molecules at different levels of structural hierarchy. Since evolutionary selection mechanisms act upon individual organisms, these organisms are the basic building blocks of any ecosystem. The success of an individual organism in dealing with its environment determines its capacity to survive and spread its off-spring.

Individuals have to accomplish multiple tasks such as photosynthesis, nutrient and water uptake, water transport, growth and mechanical support. Specialized organs (vegetative or reproductive) have developed to perform these tasks. For example, leaves perform photosynthesis, fine roots take up water and nutrients, and stems transport water and assimilates. All organs include several tissues, involved in specialized functions within the organ.

Cells are the basic building blocks of all living organisms. They often have tissue-specific features but within the plant kingdom, their basic structure is rather similar. Cells have their own metabolism, but are not independent in the sense that they need to take raw materials and information from other cells or from the environment, and

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in response they also may produce material for other cells. The inner, subcellular structure of the cell reflects the specific metabolic task of the tissue formed by similar cells.

An interesting feature of plant tissues is that living cells may be surrounded by a non-living region, the apoplast, that is never-the-less an important structure from the whole plant perspective. For example, a major part of the transport phenomena in plant (see Chapter 7) take place in the non-living tissue of tree woody axis.

Stands are formed by individuals, either trees or those of ground vegetation, interacting with each other. Trees modify environmental factors within the stand, resulting in alterations in metabolic processes, especially in the lower part of the canopy and in the ground vegetation. Furthermore, the senescing parts of living plants when falling to the ground feed the organic component in the soil.

Similarities in the physical environment of the plants generate vegetation zones on the globe. Between 50° and 70°N, the environment favors a mosaic of evergreen coniferous forests and peatlands depending on the water retention in the soil and the resulting influence on the rate of decomposition. The forested zones may be broken into forest stands of different size following the action of catastrophic disturbance events. Within these stands, trees grow and become mature and die forming more heterogeneous canopy structures over time. Silviculture has greatly changed the natural spatial dynamics of forest stands making them more homogeneous in size and internal canopy structure, and thus easier to harvest (Kuuluvainen, 2002).

5.2 Vegetation

5.2.1 Chemical Structure

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Plant cells have hundreds of different biochemical components, but the cells and organelles share many similar features in respect to their macromolecular structure. The major components are large carbohydrate molecules, which can roughly be classified as structural, functional, regulatory, storage and secondary molecules. Some of them contain only carbon and hydrogen, others have significant quantities of other molecules such as nitrogen or sulphur, which are important as functional groups of molecules (Table 5.2.1). Here we describe the chemical structure of the most important macromolecule groups in mature gymnosperm cells. In addition to general reference to Buchanan et al. (2000) and Taiz and Zeiger (2006), specific references concerning boreal tree species are given.

Table 5.2.1 Element fractions in some cellular macromolecule groups

Fraction (%)	Carbon	Nitrogen	Hydrogen	Oxygen
Lipids	75–78	–	8–11	9–17
Sugars + starch	40	–	7	52
Hemicellulose + cellulose	43	–	7	49
Lignin	67	–	6	27
Proteins	40–50	10–25	5–10	22–40

5.2.1.1 Macromolecules

5.2.1.1.1 Functional Substances

Functional substances enable, by definition, processes in living organisms. All metabolic pathways consist of several interlinked processes, involving numerous functional and regulating substances.

Proteins

Most functional substances are proteins, some of which are composed of several chemical entities which are functional only when they are together. Proteins form about one tenth of the total dry matter in living plant cells, and they can be either soluble or bound to various membraneous structures. Proteins or their parts function as enzymes, signaling molecules, structural compounds and membrane pumps. Proteins have molecular masses ranging from 1 to 10^3 kDa (Da = Dalton, the unified atomic mass unit based on the mass of a ^{12}C atom; 1 kDa $= 1.66 * 10^{-24}$ g), and they may be composed of several subunits. All proteins are formed of 20 different amino acids, which are organized into long chains called polypeptides (primary structure). There are generally 200–300 amino acids in one protein molecule, but some proteins can be considerably larger. The organization of polypeptides (secondary structure) determines the chemical and physical properties of the proteins. The three-dimensional conformation of protein molecules is determined by their folding and arrangement of atoms in the molecules, and the quaternary structure is formed when several subunits are linked together to form a functional protein.

The vast majority of proteins are **enzymes**, which act as biological catalysts in all metabolic processes that occur in living tissue. Enzymes are highly specific to their substrates and end products, which partially explains why there are so many different enzymes involved even in the simplest metabolic chains. They also have rather specific temperature and pH requirements where they can operate. Their catalytic capacity makes the enzymatically catalyzed reactions typically in the order of 10^8 to 10^{12} times faster than the corresponding uncatalyzed reactions. Isozymes are enzymes with a similar catalytic function but localized in different cellular compartments, such as, e.g., isoprene synthase which can be found both as soluble, stromal

form and as bound in thylakoids, or nitrite reductase in plastids of either roots or leaves. The amounts of enzymes in the cell compartments are determined by the relative rates of their synthesis and degradation, i.e., turnover rates of the enzymes.

The enzyme molecule has an active site where the substrate and potential catalytic groups or cofactors are bound. In the process of catalysis, the properties of the enzyme itself are not changed, although reversible changes in the conformation of the active site may occur. Most enzymatic reactions show an exponential increase in rate with increasing temperature, up to the point where the enzymes are denatured and a rapid and irreversible decline in activity results.

Of the total soluble protein in green leaves, 40–50% is in the plastidial ribulose bisphosphate carboxylase/oxygenase (Rubisco), making it the most abundant single protein in plants. Rubisco is unique in that the same enzyme catalyzes two important reactions, namely carboxylation and oxygenation. Rubisco is a relatively large enzyme (560 kDa) with eight large, chloroplast-encoded subunits and eight small, nuclear-encoded subunits. Rubisco concentration in chloroplasts is ca. $8\,\mathrm{mg\,m^{-2}}$ (based on leaf area; Warren et al., 2003).

Transport Structures

The penetration of membranes by ions, metabolites and solutes is a prerequisite for most essential cell processes, and needs therefore to be carefully controlled (e.g., Flügge, 1999; Fig. 6.3.17). Details in membrane trafficking have been a subject for extensive research in recent years, but only the general structures and phenomena are described here and in Section 6.3.2.4. The penetration of membranes by molecules is performed with the help of a variety of intrinsic membrane proteins, which function either as active pumps for hydrophilic substances, or as passive channels or carriers. Hydrophobic molecules can passively move through membranes proportional to their lipid solubility.

Membrane pumps are proteins which are essential in the exchange of molecules and ions through the semipermeable membranes separating the compartments from each other, and in controlling cell and organelle pH and osmolality. They occur e.g. in mitochondrial membranes, plastid envelopes, tonoplasts surrounding the vacuoles, and in plasma membranes. Also the nuclear envelope possesses specialized transport structures. Nuclear pores are elaborated structures of hundreds of different proteins, involved in movement of macromolecules and ribosomal subunits both into and out of the nucleus.

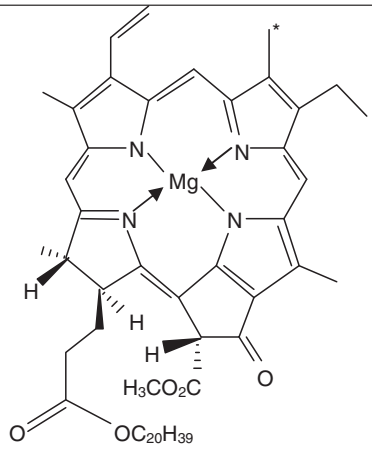
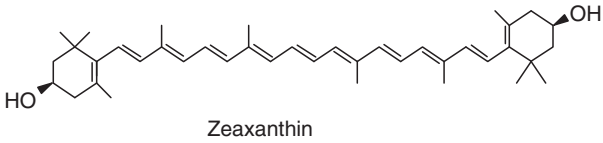
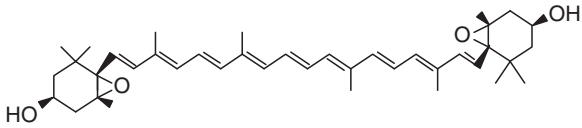
Water transport through the lipid bilayer membranes occurs via aquaporins. Aquaporins are relatively small, integral membrane proteins, belonging to a larger Major Intrinsic Protein (MIP) family of transmembrane channels. They form a selective channel for water molecules across the plasma membrane or tonoplast, and their expression and functions are controlled in response to plant water availability (Maurel, 1997). They have been assumed to form narrow pores of 0.3–0.4 nm in diameter, excluding all larger molecules than water, which would flow molecule by molecule through the pore down to the pressure gradient.

Light-Absorbing Pigments

Light quanta are absorbed in the chloroplast thylakoid **pigments** by chlorophyll *a* and *b* and carotenoid molecules in photosynthetic light reactions (e.g., Bendall, 2006). Chlorophylls (Table 5.2.2) are lipid-like molecules which form a tetrapyrrole ring with a Mg atom in the centre. The molecule is nonpolar due to its long hydrocarbon tail. Small chemical changes render the chlorophyll *a* into chlorophyll *b*, which has a different action spectrum, i.e., absorbs different wavelengths of incoming radiation. Carotenoids and xanthophylls are products of the isoprenoid pathway and can be rapidly converted to each other by changes in light intensity (see Section 6.3.3.2.1).

Photosynthetic reaction centers PS I and PS II are integral membrane protein complexes, containing both chlorophyll molecules and several electron acceptor molecules acting as converters of light energy into chemical energy in a highly

Table 5.2.2 Chlorophyll *a* and Xanthophylls and their structural formulas

Name	Molecular formula
Chlorophyll *a*	
Xanthophylls	 Zeaxanthin  Violaxanthin

organized manner. Reaction centers are localized in thylakoid membranes where they are distributed in a nonrandom fashion and interlinked by many other molecules.

In Scots pine needles the total chlorophyll content is 0.9–1.8 mmol m^{-2} (based on leaf area, Warren et al., 2003).

5.2.1.1.2 Regulating Substances

The functional substances are under strict control by the biochemical regulation system which provides homeostasis and enables the annual cycle of metabolism and acclimation to prevailing conditions. This control is achieved by regulating substances, which participate in synthesis, decomposition, activation or deactivation of the functional substances. The mechanisms to determine how regulation occurs in response to various stimuli are copious, and we present here only a rough schematic outline for the purpose of the following analyses.

We consider the regulating substances to be a very heterogeneous group of compounds, including e.g.:

- Many metabolites and proteins (for example fructose-2,6-bisphosphate, chaperones such as Hsp70, protein kinases, proteases and many other enzymes), taking part in the activation and turnover of enzymes or expression of genes
- Hormones and other signaling molecules (e.g., ethylene, polypeptides, polyamines, jasmonic acid), transmitting information between distant plant parts
- Inorganic molecules such as, e.g., NO_3^-, S, Ca or P

Regulation may take place at several different levels, from gene expression to activation of catalytic sites by cofactors. At a genetic level the amounts of enzymes are regulated by mechanisms that control expression of genomes in nucleus, chloroplast or mitochondria. Changes in protein biosynthesis also regulate enzyme concentrations, whereas post-translational modifications mostly contribute to regulation of enzyme activity. Some of the regulating substances are constitutively expressed (permanently turned on), others are inducible (involved in specific stages of development or specific environmental stimuli).

An enzyme molecule, once synthesized, has a finite lifetime in the cell, ranging from a few minutes to several days or weeks. Therefore, steady-state levels of cellular enzymes result from an equilibrium between enzyme synthesis and enzyme degradation, or turnover, which is achieved via the action of one or several regulating substances. Defective or abnormal proteins have to be disassembled to prevent the formation of large insoluble aggregates that would eventually inhibit the proper cellular functions. Protein degradation by protease enzymes also facilitates the recycling of amino acids.

One important example of post-translational regulation is phosphorylation and dephosphorylation of enzymes such as nitrate reductase enzyme in roots, which provides a far more rapid control over the nitrate assimilation process than could be achieved through synthesis and degradation of enzyme molecules (minutes *vs.*

hours) (e.g., Kaiser et al., 1999). The regulation of nitrate reductase depends, e.g., on root carbohydrate levels which stimulate the protein phosphatase activity, and consequently nitrate reductase is activated or deactivated.

Another example of metabolite-mediated regulation is the chain of reactions by which fructose-2,6-bisphosphate, a cytoplasmic sugar phosphate, regulates the carbon partitioning into starch and sucrose synthesis in green leaves (e.g., Stitt, 1990). The effect of fructose-2,6-bisphosphate is determined by the relative concentrations of activators and inhibitors, which include several Calvin cycle metabolites, inorganic phosphate and indirectly also light, through reactions associated with photosynthesis.

Signaling compounds are a heterogeneous group of molecules which are synthesized and degraded via a variety of metabolic pathways, and their pool sizes are rapidly changing (e.g., Davies, 1995; Babst et al., 2005). Most plant hormones and signaling compounds are present in tissues in micromolar concentrations. The signal is transmitted from the site of synthesis to distant parts where specific receptor molecules interact with the signaling molecule. Despite their small concentrations, they play vital roles in regulating the plant responses to environmental factors. Most importantly, they regulate cell division and extension, and more generally, growth and senescence of cells and organs. The signaling compounds include e.g. gibberellins, abscisic acid, auxin, cytokinins, ethylene, sterols and jasmonic acid.

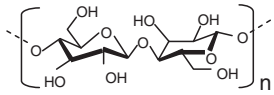
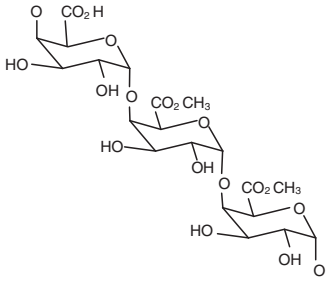
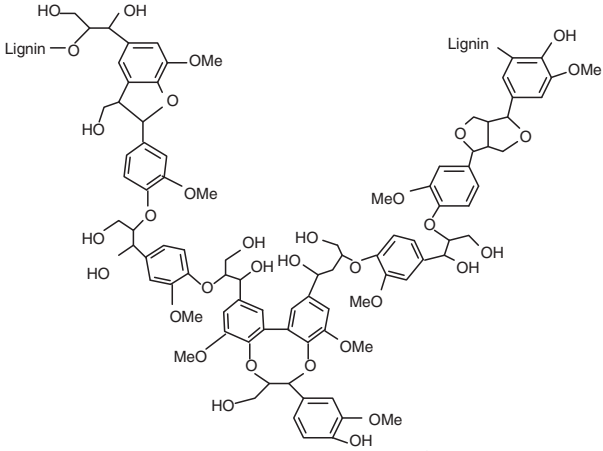
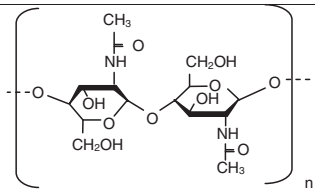
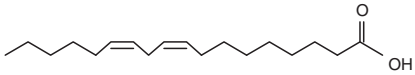
5.2.1.1.3 Structural Compounds in Cell Walls and Membranes

All plant cells are separated from their environment by the cell wall consisting mainly of a network of cellulose and lignin (e.g. Sjöström, 1993; Morrell and Gartner, 1998). Primary walls are formed during the cell division, and the complex secondary walls during the cellular differentiation. Covalent and non-covalent cross-linking between molecules is a major contributor to the structural characteristics of secondary walls. The inner side of the primary wall is connected to the plasma membrane, consisting of a lipid bilayer and embedded proteins. Also subcellular organelles are surrounded by principally similar membraneous structures.

Cell Wall Polysaccharides

Cellulose (Table 5.2.3) molecules consist of numerous (from 2,000 to 20,000) D-glucose units arranged parallel to one another and hooked together with a β-linkage into glucan chains. The linkage is unique in the sense that it forms almost perfectly straight chains. Furthermore, the chains of glucose molecules bond to each other noncovalently with H – OH-bonds, which make cellulose microfibrils insoluble in water or organic solvents, and provide the molecule's high tensile strength. Cellulose microfibrils vary in length and width, and generally compose more than 30% of the dry weight of the wall. In Scots pine heartwood the cellulose concentration varies between 130–150 $mg\,cm^{-3}$ (Harju et al., 2003). Cellulose is synthesized by an enzyme complex associated with the outer layer of the plasma

Table 5.2.3 Structural compounds in cell walls and membranes and their structural formulas

Cellulose	
Pectin	
Lignin	
Chitin	
Linoleic acid[a]	

[a]An example of a membrane fatty acid.

membrane, which means that following their synthesis, cellulose molecules are already positioned in their final location and don't need to be transported. The enzyme uses UDP-glucose as a substrate.

Pectins (Table 5.2.3) are cell wall matrix polysaccharides formed of galacturonate, rhamnose, galactose and arabinose. They comprise about 30% of the cell

wall dry weight, and participate in, e.g., modulating wall pH and porosity. Pectins in the middle lamella bind the cells strongly together by branching, aggregating with calcium ions and cross-linkages between other cell wall components.

Hemicelluloses are a heterogeneous group of tightly bound polysaccharides, which do not assembly into microfibrils but are covalently linked to lignin molecules. They are rich in glucose, xylose or mannose. The most abundant hemicelluloses are xyloglucans which can form about 20% of dry weight of the wall. In Scots pine heartwood, the hemicellulose content is ca. 60 mg cm^{-3} (Harju et al., 2003).

Lignin (Table 5.2.3) is a complex mixture of several phenylpropanoid alcohols, and due to its mechanical rigidity, it is most common in the cell walls of supporting and conducting cells such as in vascular tissue. Lignin fills the spaces between cellulose, hemicellulose and pectin components in cell wall matrix. Deposition of lignins into cell wall implies specific irreversible changes in the cells that ultimately lead to cell death, and result in the formation of wood secondary xylem tissues. Lignin partially replaces the water in the wall structure, thus increasing the hydrophobicity of the wall structures. Lignin deposits may account for about 20–35% of the dry weight of wood, i.e. 80–100 mg cm^{-3} (Harju et al., 2003). In conifer cell walls the most abundant lignin polymers are coniferyl alcohol and p-coumaryl alcohol. Particularly abundant lignin is in compression wood.

Chitin (Table 5.2.3) is the major component of cell walls in most fungi, and it occurs also in cell walls of many insect and crustacean species (Lezica and Quesada-Allue, 1990). It is a polysaccharide, formed of N-acetyl-D-glucos-2-amine molecules bound together with β-1,4 linkages, and resembles thus chemically the structure of cellulose molecule in plant cell walls. Chitin content in ectomycorrhizal roots can be used as an indicator of fungal biomass, integrated over the whole life span of the roots (Ekblad et al., 1998).

Lipids

Most lipids contain long-chain fatty acids which are esterified to glycerol, a 3-carbon alcohol. In plants, lipids are exclusively synthesized in plastids in the fatty acid pathway by cyclic condensation of two-carbon units. Their precursors can be either plastidial or cytoplasmic, and the central intermediate is acetyl-CoA, a 2-carbon acetylated compound which is one of the most central intermediates in all cellular metabolism and provides an important link between many biosynthesis pathways.

The composition of lipids varies between cellular organelles, and membrane and storage lipids often have quite distinct composition. Plasma membrane lipids are phospholipids, whereas in plastids the membrane lipids are almost entirely glycosylglycerides. Minor components are sphingolipids and sterols. In the membrane double bilayers, the lipid molecules are organized so that the polar heads in the outward facing region are hydrophilic, whereas the inner region (towards the center of the membrane) fatty acids are hydrophobic. These properties are extremely important for the membrane functions, as they prevent random diffusion of solutes

between cell compartments. The polar glycerolipids are 16- or 18-carbon straight fatty acid chains with varying degree of unsaturation, and this regulates the fluidity of the cellular membranes.

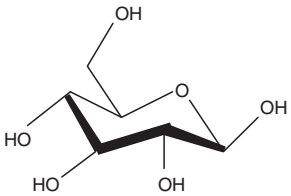
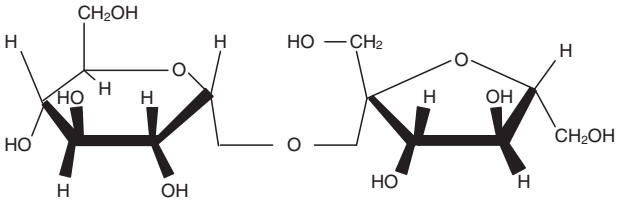
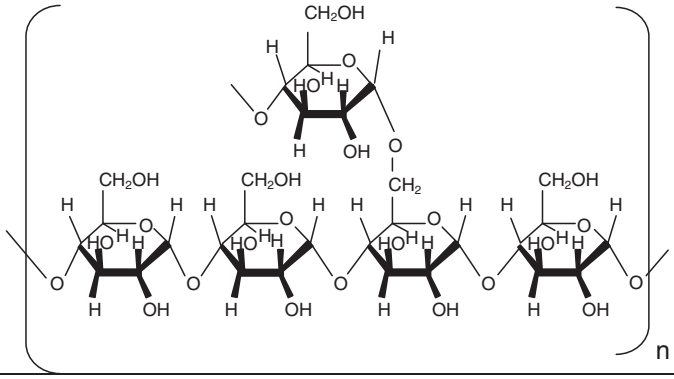
Many pigments, such as chlorophylls, plastoquinone, carotenoids and tocopherols are actually lipid-related substances, and they account for about 30% of the lipids in plant leaves. The epidermal cells are covered with an epicuticular layer (composed of a network of cutin and embedded polysaccharides, and overlaid by wax crystals) to prevent uncontrolled flux of water from the leaves. Root endodermal cells also have a hydrophobic layer composed of suberin.

5.2.1.1.4 Storage Compounds

Starch and Sucrose

The main form of carbon storage in coniferous trees is starch (Table 5.2.4 and Fig. 5.2.1), whereas the most important transportable carbohydrate is sucrose

Table 5.2.4 Glucose, sucrose and starch and their structural formulas

Glucose	
Sucrose	
Starch	

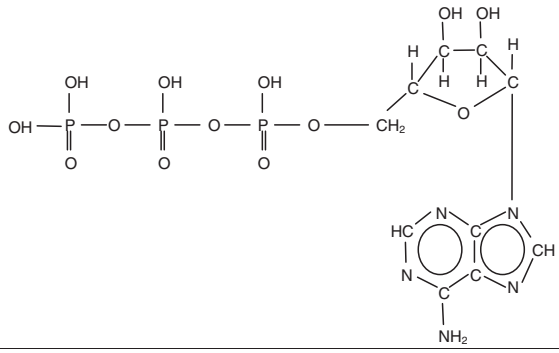
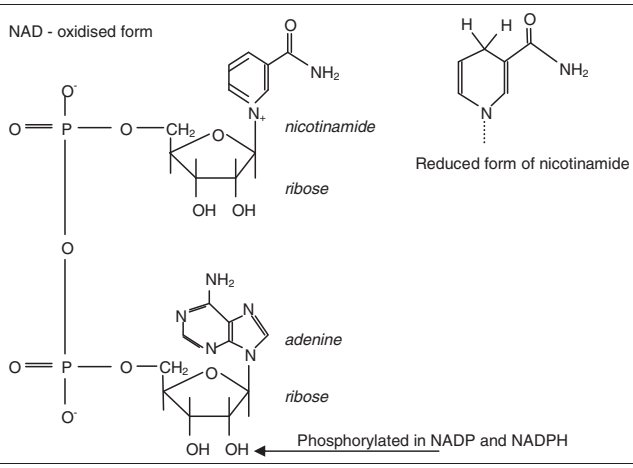
(Table 5.2.4). The syntheses of starch and sucrose are competing processes depending, e.g., on the inorganic phosphorus level in cytoplasm. Sucrose is a disaccharide and the major soluble end product of photosynthesis in green leaves.

Starch consists of two types of long carbohydrate molecules, unbranched amylose and branched amylopectin, which are formed of α-(1→4)glucose units (Table 5.2.4). Starch synthesis occurs in chloroplasts where it is also stored as large granules. Specialized storage plastids called amyloplasts serve as energy reserves in rapidly developing tissues such as seeds or buds. Starch grains vary in size from less than 1 μm in leaves to larger than 100 μm in seeds, and can grow in multiple layers. The amount of starch varies greatly within season and plant organ.

Energy Stored in ATP

ATP (adenosine triphosphate) (Table 5.2.5) is the universal energy carrier which is readily useful for fueling numerous cellular reactions. ATP is also a metabolic effector, regulating many reactions by its turnover rate. It is formed in both photosynthetic light reactions and in the respiratory pathways, and consumed, e.g., in

Table 5.2.5 ATP, NAD/NADH and NADP/NADPH and their structural formula

ATP (adenosine triphosphate)	
NAD/NADH and **NADP/NADPH**	

the Calvin cycle for reducing CO_2 into carbohydrates, and in almost all anabolic reaction chains thereafter. In the inner mitochondrial membrane and chloroplast thylakoids, the ATP synthesis involves an H^+ potential across the membrane, created by a transmembrane ATP synthase enzyme. ATP can be translocated between organelles, and especially the mitochondrial ATP-ADP translocator is an important component in cell energy balance (Hoefnagel et al., 1998).

ATP is hydrolyzed to liberate the energy and yield ADP and inorganic phosphate, which then can be recycled. Other forms of chemical energy (e.g., NAHD or $FADH_2$) need to be converted to ATP before they can be used as energy sources.

Reducing Power Stored in NADH, FADH and NADPH

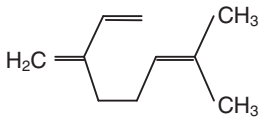
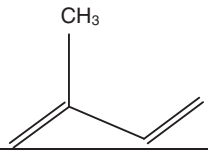
All energy demanding or binding biochemical reactions involve the formation or participation of cofactors NAD^+ (nicotinamide adeninine dinucleotide) (Table 5.2.5), FAD^+ (flavin adeninine dinucleotide) or $NADP^+$ (nicotinamide dinucleotide phosphate). These cofactors are reduced by accepting electrons and one or two protons to produce the corresponding reduced compounds NADH, $FADH_2$ and NADPH. Glycolysis generates both ATP and NADH, whereas NADPH is supplied by the oxidative reactions of the pentose phosphate pathway and citric acid cycle. $FADH_2$ participates in the citric acid cycle and oxidative phosphorylation in mitochondria.

5.2.1.1.5 Secondary Compounds

In addition to the primary carbon metabolites, plant cells include numerous compounds performing specialized functions. Although they commonly are known as secondary metabolites, the group of compounds included in this category is very heterogeneous, and many of their functions are vital for plant survival and growth. These compounds are synthesized via, e.g., phenylpropanoid, isoprenoid or shikimic acid pathways, and can occasionally form a significant sink for assimilates. One important feature of secondary compounds is that the same compounds can be either constitutive (permanent storage pool in specialized cells) or induced (temporary pool which is produced after activation of metabolic pathways). The most important group of compounds in respect to the topic of this book is isoprenoids.

Isoprenoids are a large group of carbohydrates varying both in size and in chemical structure. The smallest molecule is isoprene (Table 5.2.6), which is the basic structural component in all larger isoprenoids. Their synthesis occurs in both plastids and cytoplasm, and two partially independent pathways are involved (e.g. Kesselmeier and Staudt, 1999; Pichersky and Gershenzon, 2002). Isoprene and many other small isoprenoids such as mono- and sesquiterpenes (Table 5.2.6) are volatile at ambient temperatures, and thus tend to evaporize. Many isoprenoids are specifically synthesized for, e.g., defense purposes and stored in specialized storage tissues, although not all of their precise functions are fully elucidated to date. Recently, a protective role against high temperatures and reactive oxygen species

Table 5.2.6 Secondary compounds and their structural formulas

Myrcene[a]	
Isoprene	

[a] An example of a monoterpene.

has also been postulated for many isoprenoids. Plants produce also copious numbers of non-isoprenoid volatile compounds, which are by-products of other major biological processes such as pectin biosynthesis (methanol), fermentation (acetaldehyde), or decarboxylation of carbon compounds in cells (acetone) (Fall, 2003).

5.2.1.2 Elements in Chemical Compounds

In addition to carbon, hydrogen and oxygen, plants are composed of 14 essential mineral nutrients. Many of these are minor constituents, yet their deficiencies can produce growth abnormalities or lead to plant death, and thus maintaining balanced uptake rates is essential for the plant survival. The tissue concentrations of macronutrients range from $10^3$to 10^4 μg (g dry weight)$^{-1}$, whereas micronutrients are found in ng (g dry weight)$^{-1}$ concentrations. Many mineral nutrients are assimilated as parts of organic compounds such as chlorophyll (Mg) or calmodulin (Ca), while others maintain their ionic identity within the plant (K).

Nitrogen

From plant dry matter, nitrogen forms about 1.5%, being the most abundant macronutrient after carbon. Since leaves contain most of the functional substances rich in nitrogen, the N content in leaves can be considerably higher than that, especially in some broad-leaved trees. In conifer needles, however, the N content is normally between 1–1.5% (Helmisaari, 1992; Pensa and Sellin, 2002). Nitrogen is the main element in amino acids and proteins, and an average of 15–17% of the molecular weight of proteins is nitrogen. Nitrogen is also a constituent in many other macromolecules such as nucleic acids, nucleotides, chlorophyll and many coenzymes. A sufficient supply of nitrogen is a major determinant for plant growth, because it is needed for functional substances.

Phosphorus

Phosphorus concentration in plant tissue is around 0.2% (dry weight) and its compounds are involved in the main energy storing and transport components, namely ATP, ADP, NAPD and NADPH. Additionally, a majority of biosynthetic pathways, such as starch synthesis and degradation, nitrogen and sulphur assimilation, and biosynthesis of cell wall components and isoprenoids, involve phosphorylated intermediates. Also nucleic acids, nucleotides, phospholipids and many coenzymes contain phosphorus. P is the macronutrient which is least available from the soil for root uptake, due to its strong chemical bonds to soil clay minerals. However, the uptake of phosphorus is greatly enhanced by mychorrizal associations, and also by root exudates that release organically bound P from the soil.

Sulphur

Sulphur plays an important role in many macromolecules, and regulates, e.g., protein activity by forming disulfide bridges in molecules and participating in catalytic site formation. Further, it is needed in electron transport chain molecules (e.g., ferredoxin and thioredoxin). An important sulphur containing a tripeptide molecule, glutathione, is involved in growth, redox control and responses to many environmental stresses. Sulphur content in conifer needles ranges between 0.7–1.7 mg (g dry weight)$^{-1}$ (e.g. Manninen et al., 1997; Rautio et al., 1998).

Other Mineral Nutrients

Magnesium (Mg) is the central atom in chlorophyll molecules and is required in many enzymes involved in phosphate transfer. **Calcium** (Ca) is a constituent in the middle lamella of cell walls, required as a cofactor in some enzymes and vitally important in signaling of a variety of physical and chemical factors through Ca-channels in many membranes and the cytoplasmic Ca-binding protein, calmodulin.

Potassium (K) is required by many enzymes as a cofactor and it is essential in establishing and maintaining cell turgor. It is the most abundant cation with millimolar concentrations, and needed for example in photosynthesis, oxidative metabolism and protein synthesis.

Also **boron** (B), **chlorine** (Cl), **zinc** (Zn), **manganese** (Mn), **copper** (Cu), **iron** (Fe), **molybdenum** (Mo), and **nickel** (Ni) are essential for normal plant growth and reproduction. Their physiological roles involve participation in, e.g., protein synthesis and electron transport reactions.

5.2.2 Cellular Level

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The principal component of all living organisms is the cell, but there are several important features which characterize plant cells in particular. The general structure of plant cells and tissues in this chapter has been compiled from Taiz and Zeiger (2006), Evert (2006) and Buchanan et al. (2000). The following structural characterizations apply mostly for boreal gymnosperm tree species (and mainly the genus */Pinaceae/*), although in some cases specific structural differences compared with angiosperm species are also indicated. Specific references are added in places where detailed and/or updated information is given.

The structural properties of the most important cell components are characterized in Fig. 5.2.1 and in the following chapters.

Cell Wall

The cell wall (Fig. 5.2.1) is the strong, outermost layer of each cell in plant tissues, governing cell shape and size, but also affecting cell expansion during growth (for a review see Fry, 2001). Cell walls differ between tissue types in their chemical composition, thickness, embedded substances, and fine structure. Generally, an elastic primary wall is formed during cell division and elongation. Primary walls of plant cells contain typically 70% water, and 90% of the dry matter is polysaccharides. Secondary cell walls are much thicker and account for most of the carbohydrates in plant biomass. Secondary walls are formed after the cells have reached their final size.

The majority of cell wall carbohydrates consist of complex polysaccharides, which are covalently linked with each other. The most abundant ones are cellulose

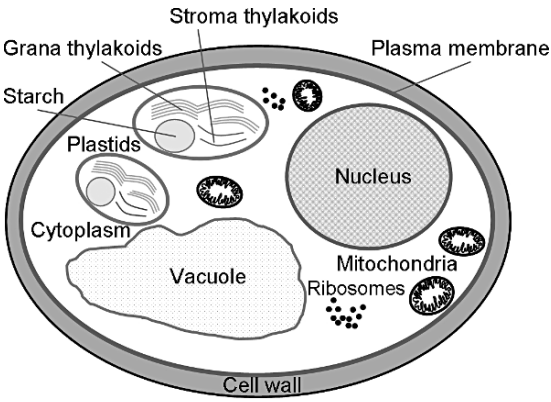

Fig. 5.2.1 A schematic presentation of the structural components typical of a plant cell. Details are given in the text

microfibrils (Table 5.2.3), forming long, chain-like layers which are embedded in hydrated, gel-like pectin (Table 5.2.3) and hemicellulose matrix. Other molecules such as suberin and cutin are deposited in those cell walls where prevention of water movement is especially important. In many secondary cell walls, especially in xylem vessels, lignin (Table 5.2.3) molecules are incorporated to improve the mechanical strength of the structure. A strong, pectinaceous middle lamella separates two adjoining cells. The inner face of the cell wall is in contact with plasma membrane, although not firmly attached to it. Meristematic and parenchymatous cells have thinner walls than collenchyma or sclerenchyma cells, and even within one cell the wall thickness can vary.

Mature cell wall generally does not participate in cell metabolic reactions. Walls allow free passage of most small, water soluble molecules and ions such as oxygen, CO_2, nitrate, phosphate, sugars and amino acids into and out of the cell, but prevent the permeation of larger molecules. Plasmodesmata (see Section 6.3.2.4 and Fig. 6.3.17) are small openings in the cell wall and plasma membrane, which form a continuum between the cells, and allow movement of water and solutes, ions and also many large molecules between the cells. The walls also have high affinity to some inorganic cations, e.g., Ca^{2+} or Cu^{2+}.

Membranes

Cells as well as most cellular organelles (e.g., nucleus, vacuole, mitochondria and plastids) are separated from their environment by a semipermeable membrane (Fig. 5.2.1). The most important functional properties of membranes follow from their biochemical nature as lipid bilayers, where large protein molecules are embedded. Proteins and lipids make roughly equal proportions of the membrane's mass. Membrane lipids (Table 5.2.3) belong to several chemical classes, including, e.g., phospholipids, galactosylglycerides and sterols, and their composition is highly variable between cell organelles and tissues, but it also varies with environmental factors such as growth temperature. Membrane proteins are either embedded into the lipid bilayer, such as proteins acting as ion pumps and receptors for signal transduction pathways, or bound to the membrane surface.

Membranes are selectively permeable to many molecules, which is reflected in their structure in many ways (see Sections 5.2.1.1.1 and 6.2.1.1). The membranes facilitate and actively control the continuous molecular trafficking as the cell/organelle takes up nutrients and metabolites, exports wastes and controls its turgor pressure. This is made possible with the specific, membrane-attached functional substances: membrane pumps, channels, antiporters and symporters (e.g. Véry and Sentenac, 2003; Weber et al., 2005; see Section 5.2.1.1.1). Membranes also form complicated internal structures, such as photosynthetic thylakoids in plastids and endoplasmic reticulum in cytoplasm, participating in many primary metabolic functions.

Plastids

Plastids are cylindrical, lense-shaped organelles which are one of the main characteristic features of plant cells. Each mesophyll cell in a mature leaf or needle contains from several tens to several hundreds of the chlorophyll-containing chloroplasts. They are arranged near the cell walls as a single-plastid layer (see Fig. 5.2.1). Chloroplasts are responsible for primary carbon assimilation, i.e., photosynthesis, and also for many fundamental intermediary metabolic reactions involved, e.g., in nitrogen metabolism. Other types of plastids are, e.g., amyloplasts (storage), leucoplasts (biosynthesis of secondary metabolites such as isoprenoids), and proplastids (the undifferentiated precursors from which all other plastids develop).

Plastids are separated from their cellular environment by a double layer membrane, a plastid envelope. The envelope, as all membranes, allows strict control of plastidial metabolism, independent from the rest of the cell. The outer and inner membranes in the chloroplast envelope differ in their composition and structure, and thus also in their functions. Surrounded by the envelope, the plastidial matrix called stroma contains a small amount of DNA, ribosomes and abundant functional substances, enzymes (e.g. ribulose bisphosphate carboxylase/oxygenase; Rubisco), as well as storage compounds such as starch and lipids. Starch grains can periodically make up the majority of the chloroplast volume.

Photosynthetic light capture occurs in chloroplast thylakoids (Fig. 5.2.1), which form a continuous network of membrane sacks, partially stacked in piles on top of each other (lamellae). Thylakoid membranes contain the photosynthetic pigments, mainly chlorophyll *a* (Table 5.2.2) and *b* and carotenoids, and their associated proteins, embedded in the glycosylglyceride bilayer. The integral membrane proteins include the photosynthetic reaction centres (PSI and PSII), ATPases and electron transport enzymes, positioned in highly specialized arrangements and unique orientation within the membrane (e.g., Chitnis, 2001; Allen and Forsberg, 2001). The majority of the pigment is clustered in antenna complexes capturing the energy of the light quanta into the reaction center complex, where the light energy is converted into chemical energy as ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate) (Table 5.2.5), simultaneously as an oxygen molecule is produced (see Section 6.3.2.3). The two photosystems and the reaction centre are closely linked with an electron transport chain which is formed of integral proteins.

Mitochondria

Mitochondria (Fig. 5.2.1) are spherical or rod-like organelles which are surrounded by a double membrane and range from 0.5 μm to 1.0 μm in diameter and up to 3 μm in length. Mitochondria are abundant in all plant cells, and they house the essential respiratory machinery which generates ATP by the citric acid cycle and electron transfer chain (see Section 6.3.2.1). Their number is closely correlated with the metabolic activity of the cells; guard cells and actively dividing meristematic cells for example are rich in mitochondria.

The smooth outer membrane completely surrounds the strongly invaginated inner membrane and the aqueous matrix located inside the double membrane. The membraneous formations of the inner membrane (cristae) contain high amounts of proteins. Small molecules can pass through the outer membrane rather freely, whereas the inner membrane has very low permeability. Mitochondria, as plastids, are semi-autonomous; they contain DNA, RNA and ribosomes and are thus able to carry out a part of their own protein synthesis.

Nucleus

Genetic codes determine all cellular functions and their responses to different regulatory agents. The nucleus (Fig. 5.2.1) is the organelle housing most of the plant genome, although plastids and mitochondria also contain a small genome of their own. The nucleic acids, **DNA** (deoxyribonucleic acid) and **RNA** (ribonucleic acid), are large polymers that store and transmit genetic information in cells. DNA constitutes the genome of the cell, and it forms the chromatin where the huge molecule is coiled in a double helix form. The three different RNA molecules contribute to the transcription, translation and processing of the encoded genetic information into protein structure. Both DNA and RNA are long, unbranched molecules, each composed of four different types of nucleotides. The nucleus is surrounded by a porous nuclear envelope, which is permeable to ribosomal subunits and some macromolecules through the nuclear pore complexes housing an active membrane transporter.

DNA comprises the chromosomal material, chromatin, which builds up genes when assembled in a highly organized manner. In chromatin, long DNA molecules are tightly packed together with proteins into a double helix structure where two DNA strands are associated with their complementary base pairs, linked with hydrogen bonds. The recently unveiled poplar (*Populus trichocarpa*) genome size is 480×10^6 base pairs (Tuskan et al., 2006); for the gymnosperm species genome, such a detailed analysis is not available at the moment.

RNA is the primary product of gene expression after DNA transcription by RNA polymerases, and it has an essential role in protein synthesis and many other cellular functions. Most of the RNA is ribosomal, i.e., bound into small, two-subunit structures which serve as platforms for reading of the information which translates into the amino acid sequence of each individual protein.

5.2.3 Tissue

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In general, the anatomy of any individual plant structure is highly specialized for some particular process or for transport. Therefore plant tissues entail specific

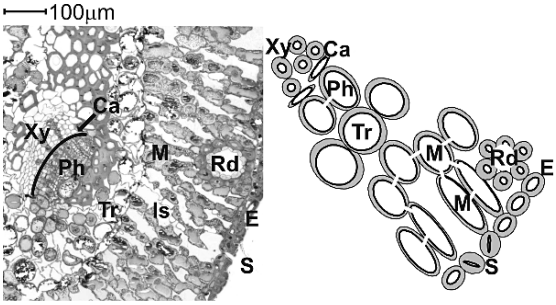

Fig. 5.2.2 Light micrograph (left) and schematic illustration (right) of epidermal, ground and vascular tissues of a Scots pine needle. Stoma (S), resin duct (Rd), phloem (Ph), xylem (Xy), cambium (Ca), transfusion parenchyma (Tr), epidermis (E), mesophyll (M), intercellular space (Is). Plasmodesmal connections are seen in (b) between mesophyll cells and between sieve elements and companion cells

anatomical and biochemical features to fulfill these functions. A tissue is considered to consist of a group of functionally similar cells, acting in concert in response to external or internal cues. The vascular plant tissues are either dermal, vascular or ground tissues, and these can be found in all organs, although in varying proportions.

Dermal tissues are the outermost layer of organs facing the atmosphere or soil. They protect the inner tissues from extreme environmental conditions, but also selectively exchange compounds between the plant and the environment. In needle-like leaves (Fig. 5.2.2), the dermal tissues consist of one or two layers of thick-walled cells (epidermis, hypodermis), which are covered with a thin cuticle and a complex, waxy epicuticular layer to prevent uncontrolled water loss and to act as protective cover. The thickness of the epicuticular layer in Scots pine needles is only few micrometers, and that of the dermal layer 30 µm (Bäck et al., 1994).

Gas phase diffusion of many substances occurs through stomata, which are a highly specialized type of dermal tissues in leaves (Fig. 5.2.3). Stomata actively control the exchange of water and gaseous compounds (CO_2, O_3, VOCs etc.) between the plant and environment. They are formed by pairs of specialized guard cells, which perceive environmental signals and control the opening of a small stomatal pore. The stomatal pore is approximately 5 µm wide when it is fully open. Stomatal density is sensitive to many environmental factors (e.g. Woodward, 1987; Woodward and Kelly, 1995; Brownlee, 2001), varies a lot between species, and in many species it also depends on the surface of the leaf. In the boreal region, the Scots pine needle stomatal density lies between 40–140 stoma mm^{-2} (Lin et al., 2001; Luomala et al., 2005; Turunen and Huttunen, 1996).

In the developing root tips the epidermis is specialized for absorption of mineral elements and water, and therefore the outer surface differs from that in leaves. Bark is the outermost layer in stems and roots of woody plants, and describes all tissues outside the vascular cambium. Outer bark of the stem, periderm, is a three-layered region of phellogen, phelloderm, and phellem (Fig. 5.2.8). Phellogen (i.e., cork cambium) produces phellem (cork) toward the outside and phelloderm (cortical

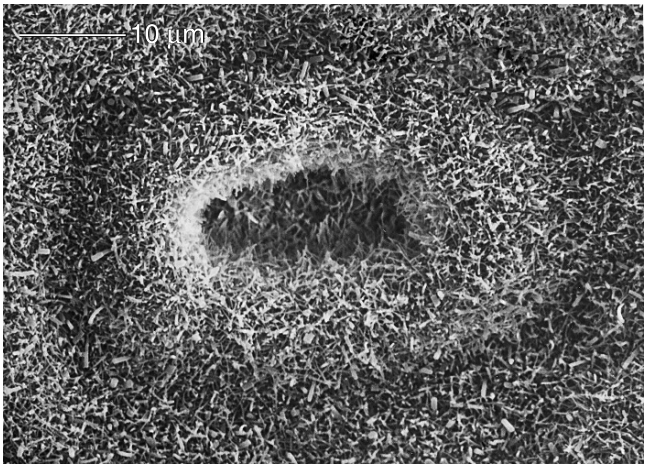

Fig. 5.2.3 A stoma of a Scots pine needle viewed under scanning electron microscope. A special feature of conifer stomata is that they are sunken deep in the epidermis, and the ledges are covered with a thick epicuticular wax layer preventing uncontrolled water penetration from guard cells (Courtesy of Satu Huttunen)

parenchyma) toward the inside of the phellogen. The cork layer is a strong tissue, and it efficiently protects the vulnerable transport tissue in stem from the external factors, and it can range from a few millimeters up to several centimeters in thickness.

Ground Tissues

Ground tissues are present throughout the plant body and formed of parenchyma, collenchyma (supporting) or sclerenchyma (protective and storage) cells. Ground parenchyma in leaves is formed from actively metabolizing cells involved in photosynthesis and storage. Most leaves have two or more layers of parenchyma cells called mesophyll cells (Fig. 5.2.4). The outermost mesophyll cell layer close to the epidermis is in many species formed by elongated, thin-walled and closely packed palisade parenchyma cells, which are rich in plastids and act efficiently in light capture and CO_2 assimilation. The palisade cell columns also channel light towards lower cell layers. In Scots pine needles, irregularly shaped and loosely arranged spongy mesophyll cells, which also photosynthesize, are located underneath the palisade tissue (Bäck et al., 1994). Light scatters in spongy mesophyll as it is reflected from cell-air interfaces, resulting in more uniform light absorption even in deeply laying cells.

In stems and roots the ground tissue is called pith or cortex, and composed of cells with thickened walls containing suberin and lignin. The detailed anatomy and location of ground tissues in stem vary a lot between tree species. In roots the central cortex usually consists of thin-walled parenchyma cells with numerous intercellular

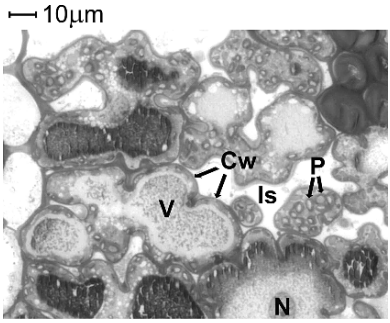

Fig. 5.2.4 Light micrograph of pine needle mesophyll cells. Vacuole (V), plastids with starch grains (P), cell wall (Cw), nucleus (N), intercellular space (Is, apoplast)

spaces. Cortical tissue allows the diffusion of water, nutrients and oxygen from the root hairs inwards, and also serves as starch reserve for root metabolism. The endodermis forms the innermost layer of the cortex in roots. Endodermal cells are more rectangular in shape, the side walls being thickened with suberin. These thickenings are called Casparian strips, and they are involved in the transport of water from cortex to the xylem.

Vascular Tissues: Cambium, Phloem and Xylem

Vascular tissues are vital for the long-distance longitudinal transport of substances within the plant individual, and they form a continuous structure from roots to leaves. In stems and needles of gymnosperms, they run parallel in a vascular bundle (Figs. 5.2.2 and 5.2.7), and in roots the vascular tissues occupy a separate central cylinder area, where xylem and phloem tissues are arranged in close connection with each other. Both tissues have primary cells that originate from recently differentiated cambial cells, and secondary cells which are metabolically mature and can form several cell layers.

The majority of the xylem in mature conifer tissues consists of thick-walled secondary xylem, where the regularly organized tracheids conduct water and solutes in the system. In the xylem of broadleaved trees the tissue is more variable, consisting of vessels, tracheids and fibers, and also the proportion of living parenchyma in wood is higher. Tracheids and vessels are dead when they reach maturity. They are predominantly vertically oriented (with exception of rays, Fig. 5.2.6) very long and narrow cells that are connected to neighboring elements by small pores (Fig. 5.2.5). Normally these cells are tens to hundreds of micrometers in diameter but may be several millimeters to centimeters long. In broadleaved trees, the vessels consist of several vessel elements and they are generally much wider and longer than the tracheids that are normally only a few millimeters long. The diameters of connecting pores are normally a few micrometers to 20 µm. In the pores there is a mesh-like structure in the direction of cell walls in the middle of the pore called margo that may have, especially in conifers, a thickening in the middle called the torus. Margo and torus are important structures in preventing the spreading of the air bubbles in the xylem vascular tissue.

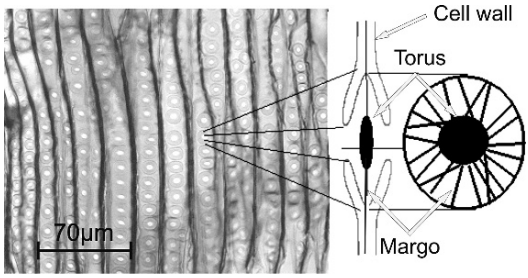

Fig. 5.2.5 A light microscope photo showing the interconduit pits in the tracheid wall of Scots pine and a schematic illustration of a pit structure with torus (black centre) and margo (surrounding net-like structure)

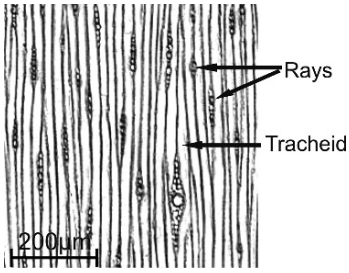

Fig. 5.2.6 A microscope photo of a tangential view of a Scots pine xylem. The groups of cells perpendicular to the longitudinal tracheids are rays with living cells (Courtesy of Tuuli Timonen)

Apart form the vertically oriented vascular tissue, xylem also has radially oriented rays that occupy from a few percent (normally conifers) up to some tens of percent (broad leaved species) of the xylem volume. In contrast to the non-living, vertically oriented vascular tissue, in ray tissue there is also living vascular parenchyma that forms an important storage of energy-rich and phenolic compounds. Radially arranged ray tracheids and associated vascular parenchyma form continuous radial channels of transport within the woody tissue extending through the xylem all the way to the phloem tissue in the bark. Thus these channels provide a symplastic connection to otherwise apoplastic wood tissue. These radial channels may have an important role in maintaining the vertical vascular tissue functional, as there seems to be at least one radial ray channel associated with each vertical vascular cell even in a conifer that consists almost entirely of numerous vertical tracheids (see Fig. 5.2.5). In conifers there are also resin ducts in the wood that are also associated with living cells.

Translocation of photoassimilates occurs within highly specialized, living phloem sieve cells (gymnosperms) or sieve elements (angiosperms). The phloem functional conduit occurs via the cell-to-cell connections at their perforated end walls or through pore-like openings in the conifers. The sieve elements are living cells although they have lost their nucleus. However, there are a number of cell organelles left such as plastids and mitochondria in a thin cytoplasmic layer anchored in the plasma membrane, and the sieve elements are thus capable of individual metabolism, e.g. sealing damaged sieve elements from the vascular connection and thus preventing leakages from the phloem. The mature sieve cells are

closely connected to large Strasburger cells, also called companion cells, which have numerous mitochondria and ribosomes indicative of high metabolic activity. The sieve cells and sieve elements and companion cells are connected to each other through a number of plasmodesmata and these companion cells have an important role in controlling the loading and unloading of sugars into the sieve cells. This is why the phloem transport tissue normally consists of sieve element-companion cell (SE-CC) complexes (Fig. 5.2.2). The plasmodesmata between the companion cells and the surrounding tissue (transfusion parenchyma) are far fewer, which is also assumed to be linked to loading and unloading processes (Fig. 6.3.17).

Meristematic Tissue

The new tree tissue is formed at specific meristematic tissues either at the ends of the growing axis (apical, primary meristem) in shoots and roots, or surrounding the xylem tissue in the growing axis (secondary meristem, or the cambium). The primary meristem gives rise to new tree organs, forming also primary wood in the shoot axis. After elongation growth in a region is complete, the secondary meristem is formed in the newly formed axis, and produces secondary phloem and xylem tissues, thus increasing the thickness of the stem or the root. Phellogen is the cork cambium which forms on the peripheral region of the expanding axis and forms periderm, a secondary protective structure to the stem. Meristematic activity is under a genetical regulation and forms a large sink for resources during the periods of active growth.

5.2.4 Organs

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The traditional characterization of vascular plant body involves the differentiation of plant parts as organs that are more or less specialized to certain functions. The main organs are stem, leaf and root, and sometimes the flowers also are considered as separate organs. The stem and leaf (and flowers) can be regarded to form the shoot (above-ground organs) in correspondence to the root system (below-ground organs). Leaves are specialized for photosynthesis, roots for anchorage, nutrient and water uptake, and the stem tissues support the above ground plant parts and form a continuum acting as pipelines for transport of water and assimilates. Structurally these organs mainly differ in the relative distribution and organization of the vascular and ground tissues.

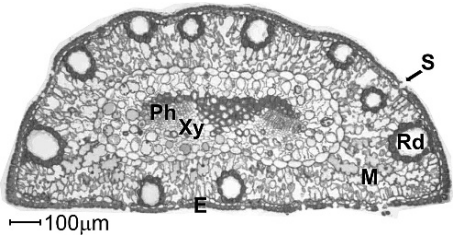

Fig. 5.2.7 A light micrograph of a cross-section of a Scots pine needle. Resin duct (Rd), mesophyll (M), xylem (Xy), phloem (Ph), stoma (S), epidermis (E)

Leaves

Leaves are the organs where light is captured for providing the energy to drive the chemical CO_2 fixation and other vital functions in plant. Leaves also participate in gas exchange between the plant and atmosphere through the stomata (see Fig. 5.2.3). Leaves can vary greatly in shape and size, but a general phenomenon is that they have a flat and rather thin leaf blade (broad-leaved species) or a thicker, cylindrical structure (needle- or scale-like leaves, Fig. 5.2.7). Usually the leaf is attached to the shoot with a petiole, where the veins connect the vasculature of the leaf to that of the shoot and further to other plant parts. The vasculature can be visible also from outside of the leaf as lateral veins and midvein in flat leaf blades, whereas in other species vascular tissues are fully embedded in the ground tissue (needle-like leaves in conifers). Leaves may be possessing external structures such as scales, hairs, glands or trichomes, mainly functioning in protection against external factors. The spatial distribution of stomata and other epidermal structures is nonrandom and a minimum spacing is existing between them. In conifer needles the stomata form several rows, where the stomata are situated 20–50 µm apart.

The leaves are usually grouped together in a species-specific manner. In many species (e.g. in the genus *Pinus*) the needles form a cluster (fascicle) consisting of two or more needles which can be from 2 up to 15 cm in length. Each fascicle is produced from a small bud on a dwarf shoot in the axil of a scale leaf. The fascicles are combined to form a unit, which consists of a group of needles of same age, i.e. they all are formed during the same growing season (or during one flush in those species having several flushes per growing season). As the shoot grows, the leaves are arranged in such a way that they tend to maximize the yield of light. Leaves can be shed annually (in deciduous trees), or sustain and maintain their vitality for 2–10 years (even 40 years in some evergreen trees). Many leaves show dorsiventral anatomy, where the leaf surfaces have somewhat different construction and may serve different functions, for example the organization of the mesophyll tissue and stomatal density may differ between the surfaces.

Leaf and shoot development is predetermined during vegetative bud development in the previous growing season in many coniferous trees, and controlled by several hormonal cues (Davies, 1995). Normally one apical and several lateral buds forming the branch whorl are formed in e.g. Scots pine and Norway spruce. The meristematic apex of the buds is very small, only about 0.1 mm high. Downwards from the apex, procambial strands, and shoot and needle primordia appear. Already the shoot

and needle primordia have highly developed vascular connections to the previous year's shoot, making carbon import possible for the needs of the developing tissues. Buds are covered by protective, waxy scales and often also by resinous excretion. The timing of shoot and needle tissue differentiation differs between boreal conifer species; e.g. in Norway spruce the protoxylem and other needle tissues are more or less fully differentiated already before bud burst, whereas in Scots pine buds and young shoots the needle tissues differentiate and their elongation growth continues longer.

Stem

The stem of a vascular plant is specialized in structural support and conducting functions between the above-ground parts (shoot) and below-ground parts (roots). Therefore the main proportion of a stem is formed of thick walled, water conducting tissue (xylem), participating in both of these functions (Fig. 5.2.8). Assimilates are

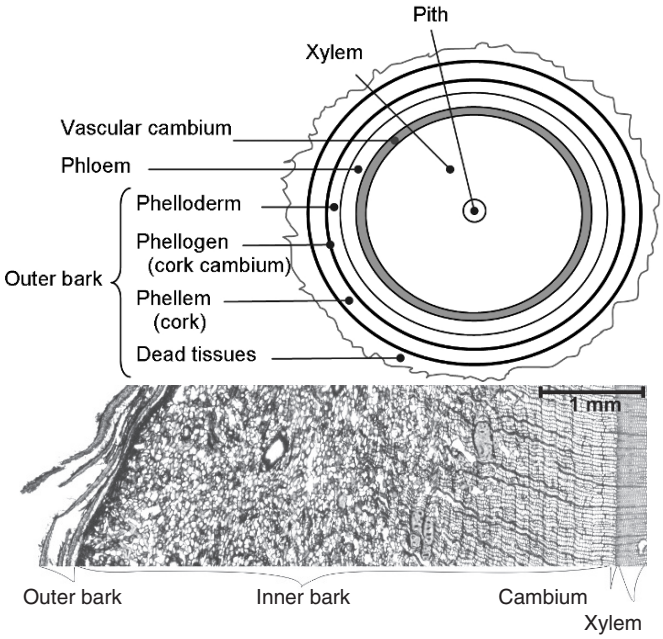

Fig. 5.2.8 Upper picture: Schematic illustration of radial components of a mature coniferous tree stem: pith, secondary xylem, vascular cambium, secondary phloem and outer bark including phelloderm, phellogen and phellem. Lower picture: The transverse, radial light micrograph is from a Norway spruce (*Picea abies* (*L.*)Karst.) Vascular cambium produces secondary xylem (only partly seen) internally and secondary phloem (i.e., inner bark) externally. Inner bark consists of the conducting, uncollapsed phloem that has functional sieve cells, and older, nonconducting, collapsed phloem. In the phloem, there are also radial rays, axial parenchyma, thick-walled, lignified sclereids, and resin canals with epithelial cells. Outer bark (also called rhytidome) consists of periderm and all tissues external to it. Periderm consists of phellogen (i.e., cork cambium) producing phellem externally and phelloderm internally (Courtesy of Tuula Jyske)

transported in the living cells of the phloem tissue, which form a minor proportion of the cross section in a stem. Stem also forms a significant storage compartment for water and reserve carbohydrates during dormancy period.

A particular feature of perennial tree structure is the capacity for growth year after year, in some cases over thousands of years. In tree stems, a lateral meristem called vascular cambium, separates the primary xylem and phloem cells of the vascular bundle. During secondary growth, the vascular cambium continuously divides to form new phloem elements to the outside and xylem elements to the inside. The cambium exhibits periodic activity forming wide tracheids with thin walls in the rapid growth during spring and early summer (earlywood). Later in the growing season, relatively narrow tracheary elements with thick walls are formed (latewood). These alternating growth phases form growth ring patterns characteristic of the woody tissues and the annual increment of the stem tissue can be measured from these rings.

The growth of secondary xylem constitutes the major part of the diameter growth in the stem, as well as in roots and branches. In conifers and in many hardwoods the living parenchyma cells in the central part of the stem die and may release secondary substances in the process of changing the chemical composition of the wood. This part of the stem is called heartwood, whereas the water-conducting part of the stem is called sapwood. The xylem cells in wood are arranged in cylinders parallel to the length axis of the stem, and the growth rings form concentric layers with alternating lumen and wall dimensions, further improving the strength of woody tissues.

The outermost layer of the stem, bark, consists all tissues out of the vascular cambium. It is consisting of the secondary phloem, the periderm (including phelloderm, phellogen and phellem) and the dead tissues lying outside the periderm. A distinction can be made between the living, inner bark, and nonliving, outer bark. The inner bark consists of secondary phloem, which is composed both of the conducting, uncollapsed phloem with functional sieve cells (gymnosperms) or sieve tube elements (angiosperms), and of older, nonconducting and collapsed phloem tissue.

Roots

Roots anchor the tree to the soil, absorb water and nutrient ions from the soil, produce many functional substances such as growth regulators, and can also store sugars and starch. Efficient acquisition of soil resources depends on both the quantity and functioning of the below-ground structures. Both non-woody and woody roots participate in water and nutrient uptake.

Most boreal forest trees possess a tap root system, where the primary root grows vertically down into the soil. Later growing lateral or secondary roots and other branches form the branching root system capable of supporting large trunks and acquiring water and nutrients from large area surrounding the tree trunk.

Roots are divided into both functionally and structurally different coarse and fine roots. Generally, fine roots (diameter <0.5 mm) located in the uppermost soil

layers are the principal sites for nutrient and water absorption, and they can account for >90% of the whole root length (Finér et al., 1997). Under drought conditions, however, the tap root system penetrating deeper into soil layers will be of greater importance.

The roots are formed by an apical meristem at root tips. This meristem is protected by a root cap surrounding the root apex. On aging, the root tissues differentiate into three anatomically different longitudinal zones: the white zone of active cells nearest to the root apex, the brown-coloured condensed tannin zone with dead cortical cells, and the cork zone characterized by a secondary growth by vascular and cork cambia (Peterson et al., 1999; Hishi, 2007). The non-woody white root tips are the main part of the absorption of nutrients occurs in most species. Behind the apical meristem there is an elongation zone, where the root elongation growth occurs by both elongation and division of cells. The elongation zone is important as the main site for root exudate liberation to the surrounding soil. This is followed by the root hair zone, where fragile epidermal structures have developed to facilitate interaction between the root and soil surrounding it. In roots, there is no waxy cuticular layer like in above ground located plant organs, but instead abundant epidermal cell extensions, root hairs, which greatly increase the absorptive area and contact with soil particles and micro-organisms.

In mature root cells of the lateral (woody) root zone, the cellular differentiation has been completed, and this has great effects on the functions of root tissue. Endodermal cells divide the root into the cortex (outside) and stele (inside), which contains the phloem and xylem tissues (Fig. 5.2.9). The endodermal cell walls contain a thin suberin layer called a Casparian strip, which acts as a hydrophobic barrier preventing the uncontrolled apoplastic movement of water and solutes across the root. Suberization of entire cortical cells in endodermis or near the rhizoderm (exodermis) may act in a like manner. Nevertheless, the endodermis and external tissues of aging roots are generally sloughed off. At this stage, the cork layer becomes the outermost layer. It is produced inside the endodermis by a cell layer called pericycle, which has the capacity to produce lateral roots and cork. Newly formed cork layer is completely impermeable against water and nutrients; cracking, dead lateral roots, and lenticells may however allow some movement of water and solutes through older cork zones (Peterson et al., 1999).

Most of the boreal woody species, including Scots pine and Norway spruce, are associated with an ectomycorrhizal symbiont, which greatly increases the effective absorbing surface area of roots and improves water and nutrient (particularly phosphorus, zinc and copper) availability for the plant, especially in non-homogeneous environments such as forests. It is commonly accepted that there is mutual benefit for the mycorrhizal partners, due to the exchange of plant-derived soluble carbohydrates for amino acids and nutrients supplied by the fungal associate (review Nehls et al., 2001).

The ectotrophic mycorrhizal hyphae form a thick sheath around the root tips and partially penetrate between the root live cortical cells, forming a net-like structure called a Hartig net. Outside of the roots, the mycorrhizal hyphae (diameter few micrometers) extend to the surrounding soil layers and form large structures inside

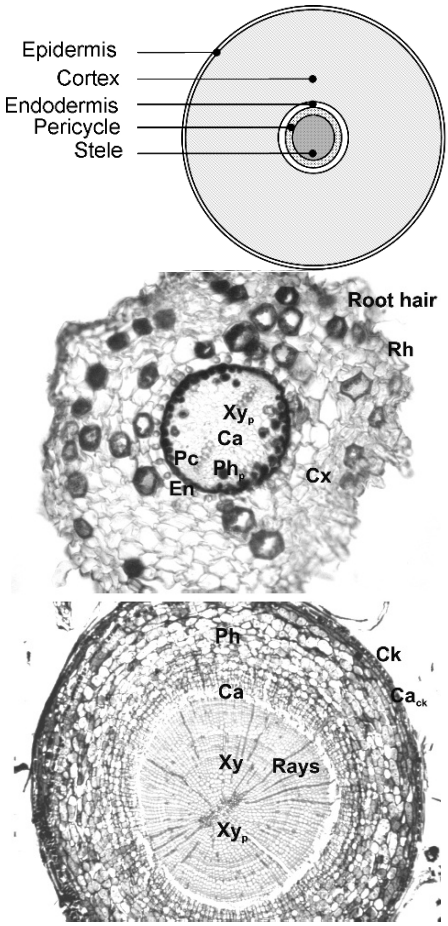

Fig. 5.2.9 Radial components of a conifer root (common yew Taxus baccata). Two upper pictures: A cross-section of a young root. Primary xylem (Xy_p), vascular cambium (Ca), primary phloem (Ph_p), pericycle (Pc), endodermis and a phi cell layer (En), primary cortex (Cx), rhizodermis (= root epidermis) with root hairs (Rh). Root diameter ca. 0.75 mm. Lower picture: A cross-section of a mature root. Secondary xylem (Xy), secondary phloem (Ph). Endodermis and external tissues have been sloughed off. Cork cambium (Cack) has arisen in a pericycle and produces a protective layer of cork (Ck). Rays extend radially across secondary vascular tissues. Root diameter ca. 2.0 mm (Courtesy of Arja Santanen)

the soil and fruiting bodies above the soil (Fig. 5.2.10). Woody plants are probably largely dependent on the symbiotic fungi to supply mineral nutrients, as there is little root surface area capable of nutrient absorption outside the fungal mantle (Taylor and Peterson, 2005).

Fig. 5.2.10 A photo of roots and mycorrhiza (Courtesy of Jussi Heinonsalo)

5.2.5 Individual

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The individual organism is the central level of the hierarchy of biological organisms, since the evolutionary selection mechanisms act upon it. The success of the individual determines its capacity for producing off-spring. A critical component of tree success is its structure. Structure determines how well trees are able to reach favorable positions in the vegetation to capture the resources it needs, how well they are able to withstand high mechanical stresses that wind or heavy snow loads can cause, and how well they balance their allocation of resources between growth and reproduction over their life span.

The central driving force for the structural development of plants is photosynthetic production. Photosynthesis takes place predominantly by leaves using the solar radiation that they intercept. However, photosynthesis also requires a continuous supply of water from other parts of the tree to the leaves, as carbon dioxide intake is associated with loss of water vapour. The detailed biological machinery responsible for photosynthesis in leaves is built up of resources that originate from soil. Thus the vascular system that supplies the crown with water and mineral nutrients, and that supplying the root system with energy and structural carbohydrates have to be developed in concert.

The particular feature of trees that distinguishes them from other plants is their large crowns and stems. An important feature of tree structure is the above and below ground architecture as it determines the extent over which trees extract

resources. Height and size are critical structural features as they determine the proportion that the individual captures from the total flux reaching the site. The architecture of the crown and root system determines the spatial distribution of the exchange sites. The closer the sites are the more they interact with each other. From the whole plant point of view this is unimportant since the resources captured are used by the same organism. However, different spatial arrangements of the exchange sites can affect the amount of resources used to bring about the uptake (e.g., Givnish, 1985; Küppers, 1989). Closely clumped structures require lower woody growth in branches and stem and even if they are not able to intercept as much light energy the saving in structural investments may make such architectural design more efficient than a more widely spread crown.

At crown level, the structure has a central role in determining the intercepted light at a certain point (e.g., Kellomäki and Oker-Blom, 1983; Oker-Blom and Smolander, 1988; Kuuluvainen and Pukkala, 1987, 1989). Closely clumped foliage will have strong internal shading while widely spread foliage does not interfere as much.

To characterize the relationship between the leaves and e.g. precipitation or light interception, a Leaf Area Index (LAI) has been widely used. LAI is generally defined as the ratio of total upper leaf surface of vegetation divided by the surface area of the ground. Usually LAI means one-sided leaf area but the meaning is not unequivocal with conifers: definitions of total, half or projected needle surface area are used as well. With needle leaves, the specific leaf area (SLA) is commonly used too. SLA is the ratio of projected leaf area to leaf dry mass.

Distribution of LAI can be derived from the height distribution of leaf mass and the leaf geometry, which usually vary in different parts of the crown: e.g. big needles have less surface area in relation to mass than small needles. LAI can be determined also indirectly by measuring the light extinction in the canopy (Chen et al., 1997).

LAI changes over the growing season as new leaves and needles emerge, and old ones are senescing and dropped down. In coniferous forests the seasonal changes in LAI are far less than in deciduous forests, due to the long-living, evergreen foliage of most conifers. Figure 5.2.11 demonstrates a needle mass distribution within the canopy in a 40-years-old Scots pine stand in Southern Finland. The average LAI in boreal needle-leaved forests is 3.5 ($\pm$3.3) $m^2\ m^{-2}$ (Scurlock et al., 2001; Global leaf area index[1]). Crown architecture is a major determinant for the radiation intensity distribution within the crown, and therefore LAI is a very commonly used characteristic to describe the light environment inside and below canopy. As the light response of photosynthesis is saturating, different shading patterns within the crown may bring about different productivity per leaf area. Narrow leaves far apart will have large penumbra area, i.e., shading only part of the sun disk while wide leaves close to each other will have very patchy light environment with bright and deeply shaded areas (Horn, 1971). In the former case the light is more evenly distributed within the crown, enhancing the production efficiency in comparison to the latter case.

[1] Global Leaf Area Index Data from Field Measurements, 1932–2000
http://daac.ornl.gov/VEGETATION/lai_des.html

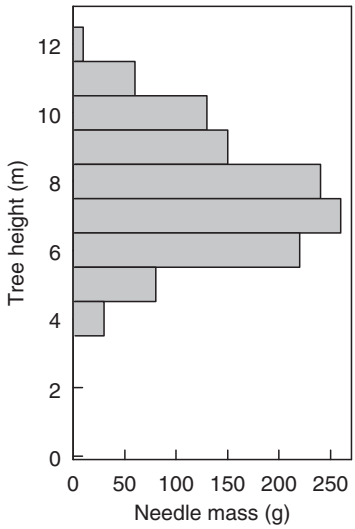

Fig. 5.2.11 Average needle mass distribution at SMEAR II measuring station in a 40-years-old Scots pine stand (Redrawn from Ilvesniemi and Liu, 2001)

Tree and canopy structure can also be viewed from the point of view of the developmental processes that brings it about or from the functional significance that the structure has. From the developmental point of view a tree is simply a collection of elementary units that form larger structures (branches etc.) over passage of time (Prusinkiewitcz and Lindermaier, 1990). Analyses of plant architecture have suggested a number of possible elementary units, such as the metamer and growth unit (Caraglio and Barthélémy, 1997; Room et al., 1994). A metamer is defined as an internode with axillary bud(s) and leaf (leaves) in its upper end, but without any shoots resulting from growth of the axillary buds (Caraglio and Barthélémy, 1997). A growth unit, initially called a unit of extension by Hallé et al. (1978), is the part of the shoot resulting from uninterrupted extension growth. Room et al. (1994) describe it as "extension of the contents of a previously dormant apical bud followed by growth of neoformed leaves (if any) and formation of a new, dormant, apical bud".

The crown structure has a dual role in a tree's life. On the one hand it influences the energy capture for photosynthetic production and on the other hand it influences the way in which a tree can exploit space in the future. Tree crown is formed as a result of reiteration of bud formation, their activation and flushing, axis growth and new bud formation. Successful tree development seems to presuppose that only a few specific buds grow and the rest either become dormant or abort (Stafsform, 1995). Depending on the competitive environment, different height growth strategies and thus also bud formation and activation, are favoured (Givnish, 1995). Shoots grown in the upper and lower parts of the tree crown play different roles in crown dynamics. Because young, first-order shoots in the upper crown are unlikely to be immediately shaded, they play an important role in supporting tree structure for many years. They will be incorporated in the structures that will provide material for the active crown above for many years. On the other

hand, shoots in the lower crown, even if at first in a strong light environment, become shaded and are less able to support other shoots and are more likely to be structures that a tree can shed.

Tree stems and crowns reflect their past developmental history, in that sense they are unique. However, a closer look at the stems reveals repeating patterns in different species. This is quite natural as tree stems have certain functional requirements that they need to fulfill. Already in his notes, Leonardo da Vinci (MacCurdy, 2002) put forward the concept that was later called the pipe model theory (Shinozaki, 1964a, b). This observation has shown that there is a constant relationship between the sapwood area and foliage area above in many species. Therefore, stem thickness increases from the tip of the tree crown downwards, in a saturating manner, as the foliage area above accumulates. Below the living crown, the sapwood area should not increase anymore according to the pipe model principle, but the whole stem thickness should increase. This is due to accumulation of disused pipes into the stem, in conifers very often into distinctly distinguishable heartwood.

This structural linking between the wood and foliage produces, at least qualitatively, the well known tapering of tree stems. However, quantitatively the assumptions of pipe model do not exactly hold below the crown or even within the crown. Below the living crown it has often been observed that the sapwood thickness, rather than area, seems to remain constant (Longeutaud et al., 2006) or even within the crown there seems to be variation in the relationship (Berninger and Nikinmaa, 1994). However, in many coniferous species, such as Scots pine, the relationship seems to be fairly constant when measured at the same reference point (e.g., below crown) in trees grown in very different growing conditions and positions within the same climatic zone.

A number of structural changes occur in the longitudinal direction in conifer stems and also from the core of the stem outwards. In the upper part of the stem the annual tree rings are wider, with considerably thinner sections of latewood than at the base of the stem. In wood technology, the wood within the crowns of fairly young trees is commonly referred as the juvenile wood. It has also been observed that the average size (length and thickness) of tracheids in the conifers become larger as the cambial age, i.e., the number of years when the cambium was initiated, increases. This observation is in agreement on theoretical derivations of structural scaling of all living creatures where the transport of substances equal to different tissues is fundamental to maintain metabolic activities (West et al., 1997).

Also the mechanical properties of xylem tissue change as a function of cambial age. The elasticity of wood rapidly decreases as the cambium ages until a rather constant value is reached (Mencuccini et al., 1997). The wood dimensions seem to follow also the requirement to withstand mechanical loads as they follow the pipe model principle. Critical factors are the diameter reference point and its distance from the centre of the loading point. A common feature in many species is the formation of so-called reaction wood at places which are under strong mechanical stress. In reaction wood the cell wall thickness normally increases vs. the lumen size in comparison to normal wood.

5.2.6 Stand

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Groups of rather even-aged trees growing on similar soil are known as stands, and they can be easily recognized in boreal forests. A stand is usually dominated by one species, although often other species are present in low numbers. During the stand development, the trees grow in height and diameter, but simultaneously the difference between big trees and small trees becomes larger due to the competition. Eventually the smallest trees start to die because of insufficient light for photosynthesis and lack of nutrients or water. This kind of orderly changes in the composition or structure of a stand is called succession.

Tree stands are structurally clearly distinguishable units in the landscape. The structural features that set the stands apart are the species composition and the tree size distribution. The reasons for the spatial differences of these features lie in the edaphic growing conditions of trees and the disturbance history of the region. A common feature of the boreal landscape is the alternation of lakes, wetlands and uplands that form a mosaic of site growing conditions. Superimposed on these site dependent differences is the impact of the disturbance history. Forest fires of different intensity, storms and large scale insect outbreaks create areas with different number and size of remaining trees of different species. These sites are gradually further stocked with newly-born and often fast-growing trees. More protected areas remain uninfluenced by the large scale disturbances and there only internal dynamics of gap establishment, growth, site dominance and tree mortality create vertically very heterogeneous stand structures with a small number of very large trees and increasing number of smaller trees. Due to the variation of factors causing the stand properties to vary, also their size variation in the landscape in the natural forests is large.

Most well-stocked stands, in terms of tree stem biomass, are the result of strong and large scale disturbance that has created fully-stocked rather even-aged stands where all the trees have established approximately at the same time. The proportion of these types of stands have increased due to silvicultural practices in the boreal region that try to mimic this type of stand development dynamics so that they are by far the most common stand structure presently, particularly in Fennoscandia (Kuuluvainen, 2002).

Within a tree stand, trees interact with each other via shading or via competition for nutrients and water in the soil. Competition for limited resources starts when the domains of resource uptake overlap (Walker et al., 1989). In a structurally heterogeneous stands there are clear differences between the trees both in terms of their height and biomass which quite clearly determines their competitive status. The development of a small understorey sapling into a canopy tree require several incidents of gap opening (Canham, 1985). In the case of even aged stand development, the trees in the stand develop together and the differentiation into size classes

results from the competition. Simultaneously with the size increase the number of trees decrease due to self thinning that can be described with a power relationship between the tree number and their average size (Zeide, 1987).

The competition for light drives the differentiation between trees in closed canopies so that small differences in height are quickly reflected on the captured energy and growth that further increase the size differences leading into vicious circle and eventual death of the most suppressed individuals. Particularly light demanding tree species allocate more of their growth into height extension than canopy width, foliage biomass and stem thickness when shaded (Vanninen and Mäkelä, 2005; Ilomäki et al., 2003) that maintains the differences between trees in the stand always more prominent in leaf area, total biomass and stem thickness than in height. This competition is a continuous process during the first 100 years of stand development in boreal forests as the individual size of trees increase, however slowing down as the tree size increase. Because of the continued change, there is always a number of different sized trees present in the canopy layer that are the same age despite their size differences. These size differences have been used in silviculture to divide the canopy into dominance classes and as the basis for different silvicultural treatments.

As a typical example, an even-aged pine stand has grown around the SMEAR II measuring station (Section 2.5.1). Its age was estimated to be 40 years when it was measured in autumn of 2002. Within a circle of radius 100 m, five size classes of trees were determined according to their diameters, and five trees were chosen as samples from each of the five classes. The annual height and radial increments were measured back to the age of three years in each size class.

The height developments in each size class were very similar and the biggest trees at 40 years were also the biggest at the age of three years and retained their ratios respectively to other size classes (Fig. 5.2.12A). The diameter development was similar to that of height development. However, the differences between size classes were larger (Fig. 5.2.12B).

Ground vegetation typically covers the forest floor level. The species composition and density usually changes during the growth and environmental effects of surrounding trees. In the early phases of succession, the radiation environment is unshaded and fast-growing and opportunist species with rapidly reproducing new tissues are dominating. Such opportunist species are e.g. *Deschampsia flexuosa, Calamagrostis* spp., *Epilobium angustifolium* and *Rubus* spp. After 10–15 years, seedlings start to shade the ground level. Then evergreen and slowly growing species are more competitive than the earlier pioneer species. Such evergreen species are e.g. *Vaccinium* ssp. (Fig. 5.2.13), *Calluna vulgaris, Rhododendron tomentosum* and mosses (e.g. *Pleurozium schreberi, Polytrichum* spp., *Dicranum* ssp.).

The species composition and density of ground vegetation are spatially very heterogeneous in all phases of succession. Small disturbances like thinning, windfall or insect damage generate living space and locally improve living condition in the environment at ground level after the death of even a single tree. Stones and boulders are typical for areas which underwent glaciation. Mosses and lichens grow on stones,

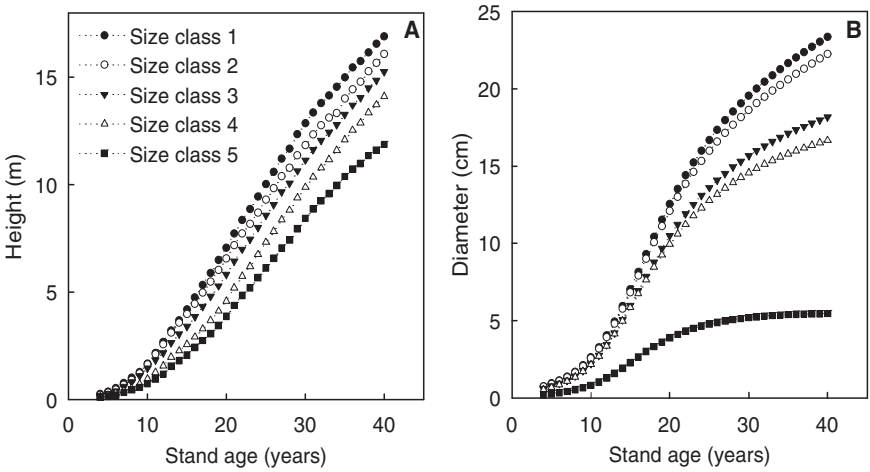

Fig. 5.2.12 The height (A) and diameter (B) development in five size classes in the stand around SMEAR II

Fig. 5.2.13 Ground vegetation at SMEAR II dominated by *Vaccinium vitis-idaea*

unlike vascular plants they do not require soil as a substrate. Small differences also in soil characters affect ground vegetation more notably than trees which are usually dominated by only one tree species and therefore have no interspecific competition. Under a homogenous tree canopy, ground vegetation type can vary and consist of small areas of diverse types of vegetation depending on small-scaled differences in water holding capacity and radiation environment.

5.2.7 Boreal Zone

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Boreal Forest Zone

By the boreal forest, we mean the set of coniferous forest ecosystems that can survive in northern, specifically subarctic, regions. Covering most of inland Alaska, Canada, Sweden, Finland, Norway and Russia, parts of the northern continental United States, northern Kazakhstan and Japan, the boreal forest is the world's largest terrestrial biome (Fig. 5.2.14). The boreal forest zone covers circa 15% of the Earth's land area and the zones of the boreal forest are the largest biome in the world.

The temperature regime in the boreal forest is variable across the latitudinal gradient. The mean annual temperature is low, and also the amount of precipitation and the climate is mostly continental. Winter temperatures fall to between −50°C and 0°C. The summer in Siberia is short, rather warm and sunny. The Atlantic cyclones cause an unstable climate with more rain in European boreal forest zones than in others (Hytteborn et al., 2005). The mean temperature in July varies between 10°C and 22°C in Siberian boreal forest zones. The annual precipitation amounts in general between 300 and 600 mm.

The boreal forest belt in Eurasia is over 1,000 km wide; in some areas reaching 3,000 km. Different classifications of zones try to describe regional variations of climate variables. The main principle is to divide boreal zones latitudinally into subzones and longitudinally into sections (Ahti et al., 1968). High topographic vari-

Fig. 5.2.14 The boreal forest zone
(Source Wikipedia: http://en.wikipedia.org/wiki/Image:Taiga.png)

ation creates problems with the zone classification approach (e.g., Norway is the area with the most complex topography and consequently is difficult to classify by zones).

In the southern parts of boreal forest we see transition between temperate and boreal forest called hemiboreal. Those forests are dominated by coniferous species, but the presence of hardwoods (angiosperms) changes the main characteristics of ecosystems. These temperate species diversify tree stand composition. This zone is called boreo-nemoral or hemiboreal (Ahti et al., 1968). In the north the boreal forest is smoothly changing into the tundra vegetation type, and the transition zone between boreal forest and treeless tundra is called forest-tundra.

Much of the boreal forest was glaciated over 10,000 years ago. Glaciers left depressions in the topography that have since filled with water, creating lakes and bogs, found throughout the boreal forest. Most of the Eurasian boreal forests are situated far from the sea and form a fine pattern of lowland forests and wetlands (Hytteborn et al., 2005). The positive precipitation balance and pure runoff from the wetlands results in humus accumulation and formation of raw humus and peat are characteristic of boreal forest zone wetlands.

Boreal forests are characterized by a low below-ground temperature. The permafrost forms as a maximum effect of a low mean annual temperature and very low winter temperatures. The permafrost stage coincides with the inception of palsas and peat plateaus (Bhiry et al., 2007). Low soil temperatures hinder the development of soil, as well as the ease with which plants can use its nutrients. Soils of boreal forest tend to be young and nutrient-poor; they lack the deep, organically-enriched profile present in temperate deciduous forests. Soil formation can be characterized by the podzolization process: the acidic reaction of decomposed litter causes leaching and moving of minerals at the top of the soils, resulting in a light horizon just below the litter (Kaurichev et al., 1989; Section 7.4).

Successional trends in boreal forest zones depend on disturbance regimes. Forest fires, windfalls and impact of humans and herbivores are main factors causing drastic changes in the forest community. Changing climate will affect the fire danger levels in boreal forests: more fire activity can be predicted (Stocks et al., 1998). Fire frequency has been determined as the main successional factor in boreal forest zones of North-America (Brassard and Chen, 2006).

Flora

The number of tree species forming the forest is rather low. Dominating species belong to the genera *Abies, Larix, Picea* and *Pinus*. Also deciduous species (*Alnus, Betula, Populus*) are represented in the composition of stands, particularly after disturbances like fires, windstorms or clear cuts where most if not all trees are removed from an area of forest. The volume of tree trunks can be as high as 400 $m^3\ ha^{-1}$ and needle mass can be 10,000 $kg\ ha^{-1}$.

The conical or spire-shaped dark coloured needle-leaf trees are adapted to the cold and the physiological drought of winter (when soil is frozen) and to the short

growing season. The conical shape of trees help them shed snow and prevent loss of branches. Needles usually also have a thick waxy cuticle. Leaves may survive for several years and the perennial foliage allows plants to photosynthesize as soon as temperatures permit in spring.

Ground vegetation in boreal forests is usually species-poor. Most common species are evergreen: low shrubs, mosses and lichens. In nutrient poor sites, dwarf-shrubs dominate the field layer. The ground layer is often conspicuous and dominated by mosses and/or lichens and covers the ground completely as a dense carpet (Hytteborn et al., 2005). However, the ground vegetation can provide much more information and more effectively express biotope conditions, therefore it has been used in site type classifications (Frey, 1978). The life history characteristics determine the sequence of species in a particular site. In comparison with other biomes the boreal forest has a low biological diversity.

Fauna

The boreal forest is the home environment of large herbivorous mammals and smaller rodents which also have adapted to the harsh climate. Moose, caribou, hare, lemmings, and voles are common herbivores in the boreal forest. Fur-bearing predators like the lynx, bear, wolves and members of the weasel family are characteristic of the boreal forest. Insect-eaters birds are migratory and leave after the breeding season. Seed-eaters and omnivores tend to be year-round residents.

The boreal forest zone in Eurasia stretches from Siberia to European North. Also the term "northern coniferous forest" refers to forest ecosystems in the north of Eurasia (Hytteborn et al., 2005). The Russian word "taiga" was first associated with coniferous forest by Siberians. Today the word has obtained a more general meaning, referring to different forests of the Northern Hemisphere.

5.2.8 Quantitative Description of Vegetation Structure

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The basic quantitative characterisation of plant structures is mass, i.e., dry weight since water content is very variable and fresh weight does not properly describe the stable structure of cells, tissues and individuals. Dry weight can be a useful measurement for tissue, individual and stand level. Sometimes a chemical characterisation using proteins, cellulose, lipids, or lignin may provide additional information. Especially the proteins, which are functional substances, are useful to treat separately.

Quantitative descriptions at tissue element level require definition of a new concept, mass density which is denoted with ρ as in physics. Consider a small space element around a point x, denote its volume with ΔV and the mass of vegetation in the space element with $m(x, \Delta V)$. The mass density, ρ, is defined as the limit of the ratio $m(\Delta V)$ and ΔV, when the volume ΔV approaches zero, in mathematical terms

$$\rho = \lim_{\Delta V \to 0} \frac{m(x, \Delta V)}{\Delta V} \tag{5.2.1}$$

When the mass density is determined at points in the canopy, we get density distribution, i.e., the density as a function of space. This enables a very detailed description of the structure in the canopy.

It is often reasonable to assume that the canopy is horizontally homogenous, i.e., objects at the same height in the canopy are so similar with each other that we can pool them together. Then the mass height distribution, ρ_h, is introduced to describe the canopy structure. Let $m_h(h)$ denote the mass below the height h. The mass height distribution is defined as the height derivative of the mass below a certain height, with mathematical symbols

$$\rho_h(h) = \frac{dm_h(h)}{dh} = \lim_{\Delta h \to 0} \frac{m_h(h + \Delta h) - m_h(h)}{\Delta h} \tag{5.2.2}$$

When the mass height distribution is determined in practice, then the canopy is divided into thin layers having the thickness Δh and mass is measured in each layer. The mass height distribution is obtained with the right-hand side of the above equation.

In the rest of this book, the structural features are expressed using the notation introduced in this chapter. When the spatial distribution of the mass density of the vegetation elements are linked to the metabolic functions of these elements and transport between them the dynamic description of structural development can be obtained. Of course the metabolic activity of each vegetation element depends on their structure at different level of hierarchy. The challenge for the dynamic description of structural development is to select an appropriate detail of description that facilitates the consideration of most significant features.

5.3 Structure of the Atmosphere

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Earth's atmosphere contains roughly 78% nitrogen, 21% oxygen, 0.93% argon, 0.04% carbon dioxide, and trace amounts of other gases, in addition to about 3% water vapor. The mean molar mass of air is 28.97 g mol^{-1}. The average atmospheric

pressure at sea level, is about 101.3 kPa. Atmospheric pressure decreases with height, dropping by 50% at an altitude of about 5.6 km and 90% of the atmosphere by mass is below an altitude of 16 km. The pressure drop is approximately exponential, so that each doubling in altitude results in an approximate decrease in pressure by half.

The molecules/atoms that constitute the bulk of the atmosphere do not interact with infrared radiation significantly. The gases that effectively absorb the long-wave radiation emitted by the Earth's surface and emit themselves the long-wave radiation both upward and downward, contribute to greenhouse effect by the downward part of the emitted radiation, thus warming the Earth's surface. Without greenhouse gases the average temperature of the surface (15°C) would be 33°C lower. In the Earth's atmosphere, the dominant greenhouse gases are water vapor, carbon dioxide, and ozone (O_3). Water has multiple effects on infrared radiation, through its vapor phase and through its condensed phases in clouds. Other important greenhouse gases include methane, nitrous oxide and the chlorofluorocarbons.

Troposphere

The troposphere is the lowest layer of the atmosphere starting at the surface and going up to about 10 km at the poles and 15 km at the equator. The troposphere is vertically well mixed due to solar heating at the surface. It contains approximately 75% of the mass of the atmosphere and almost all the water vapor and aerosol.

In the troposphere, temperature decreases at an average rate of 6.5°C for every 1 km increase in height. This decrease in temperature is caused mainly by adiabatic cooling of air when an air parcel moves upward and pressure decreases. Dry adiabatic lapse of temperature occurs under unsaturated conditions at the rate of $9.78°\mathrm{C\,km^{-1}}$ (Section 3.1). The average lapse rate is lower because of inversion layers occurring in the atmosphere and release of latent heat in saturated air conditions. Temperature decreases at middle latitudes from about +17°C at sea level to approximately −52°C at the beginning of the tropopause, separating the troposphere and stratosphere. At the poles, the troposphere is thinner and the temperature only decreases to −45°C, while at the equator the temperature at the top of the troposphere can reach −75°C.

The lower part of the troposphere, where friction on the Earth's surface influences the air flow, is the planetary boundary layer, also known as the atmospheric boundary layer (ABL). The behavior of ABL is directly influenced by its contact with the surface, and it responds to surface forcings such as surface heating or cooling in a timescale of an hour or less. In this layer physical quantities such as flow velocity, temperature, moisture etc., display rapid fluctuations (turbulence) and vertical mixing is strong. Above the ABL is the free atmosphere where the influence of surface on wind direction is negligible. The free atmosphere is usually non-turbulent, or only intermittently turbulent.

There are two principal types of atmospheric boundary layers: the convective planetary boundary layer (CBL) is the ABL where heating and evapotranspiration at the surface creates thermal instability and thus generates turbulence. The CBL is typical in summer hemisphere during daytime, when turbulence tends to mix air properties and quantities such as conservative concentrations and potential temperature are close to constant. An atmospheric layer with uniform air properties is called the mixed layer (ML). ML is frequently used as a synonym for CBL. The ABL is separated from the rest of the troposphere by the capping inversion layer – the stably stratified layer that limits exchange between the ABL and free atmosphere above. The CBL height varies from a few hundred meters during the early morning development stage up to 2–3 km in midafternoon. Occasionally solar heating assisted by the heat released from the water vapor condensation could create such strong convective turbulence that the CBL penetrates deep into the troposphere.

The stably stratified atmospheric boundary layer (SBL) is the ABL where negative buoyancy flux at the surface damps the turbulence. The height of the SBL is not well defined as the turbulence levels decrease gradually with height and the state of the SBL depends very much on the history of the ABL evolution. The SBL is solely driven by the wind shear turbulence and hence the SBL cannot exist without free atmospheric wind. The SBL is typical in nighttime at all locations and even in daytime in places where the earth's surface is colder than the air above. The SBL plays a particularly important role in high-latitudes where the long-lived (days to months) SBLs result in very cold air temperatures during winter.

In high-pressure regions, typical ABL diurnal development occurs according to Fig. 5.3.1. During the night, a stable stratification is formed due to radiative cooling. With sunrise, surface heating begins and a new shallow ML is formed close to the surface. The ML continues to grow via entrainment of air from above the ML. After the ML has eaten up the stable layer, fast growth of the ML through the residual layer occurs (which has near-neutral stratification and therefore little energy input is needed to mix the layer).

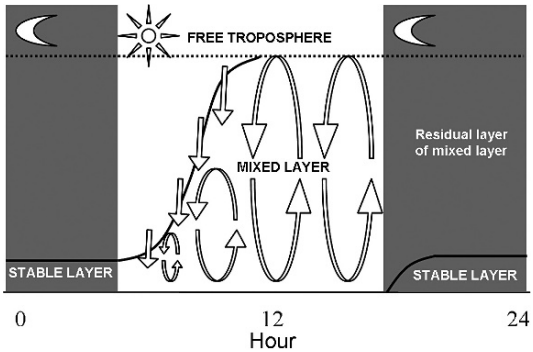

Fig. 5.3.1 Schematic picture of atmospheric boundary layer diurnal development during high-pressure conditions. The daytime convective boundary layer is separated from the free atmosphere by capping inversion layer

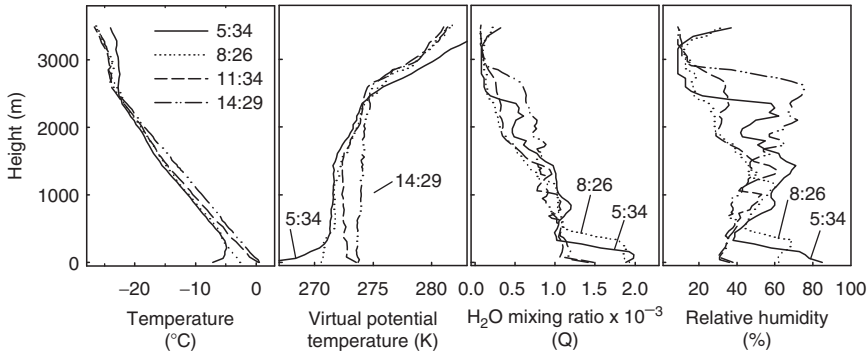

Fig. 5.3.2 The vertical profiles of temperature, virtual potential temperature, water vapor mixing ratio and relative humidity by height from four radiosondes launched at SMEAR II in Hyytiälä, Southern Finland, on April 4, 1999

With sunset, surface cooling by thermal radiation initiates formation of SBL close to the surface. Above the SBL, the residual layer of the previous day's ML persists.

Diurnal variation of the ABL height and mixing influence strongly the humidity and concentrations close to the surface. During the day ABL is deep and very well mixed, thus surface emissions are diluted and concentrations are low. At night, in turn, mixing is weak and high concentration levels occur for compounds with emission at the surface.

Figure 5.3.2 shows the vertical profiles of temperature and water concentration and development of these profiles during ABL growth periods. Except close to the surface in early morning, where the lower layer is very strongly stratified (the SBL), temperature decreases with height. Temperature decrease is due to pressure and corresponds to dry adiabatic cooling of air.

The virtual potential temperature, which takes into account the pressure reduction with height as well as the influence of air water content on the density of air, is a direct measure of stability of atmospheric layers. Around mid-day, the virtual potential temperature indicates mixing of BL up to about 1,500 m, which is the height of the ML. Also the water vapour is well mixed in this layer. Solar heating together with boundary layer development and stratification effects causes strong diurnal variation of temperature and concentrations in ABL, especially close to the surface.

At the top of the ABL, a capping inversion layer exists. In virtual potential temperature profiles, Fig. 5.3.2, the stable stratified layer above a ML rises together with ML growth until the ML depth is about 2,500 m in the afternoon. By that time the ML is covered by a strong inversion layer above.

The layer at the surface proximity where turbulence is produced by velocity gradient is conventionally called a surface layer – the lower part of the ABL. The surface layer constitutes about 10% of the total ABL depth. In the surface layer the wind profile is approximately logarithmic. However, stability affects strongly

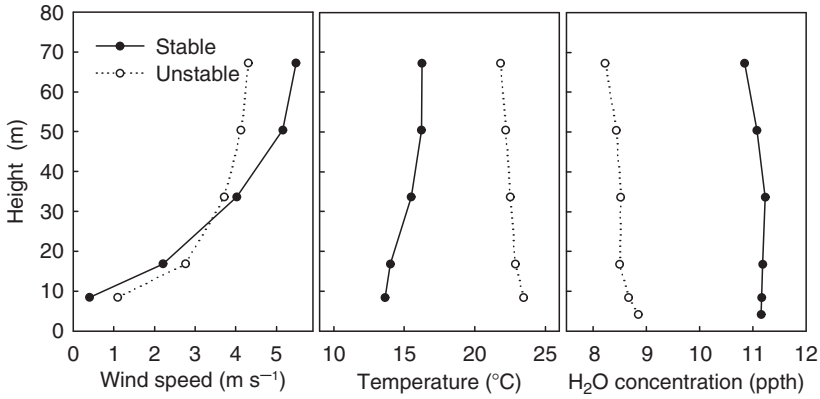

Fig. 5.3.3 Vertical profiles of average wind speed, temperature and water vapor concentration at day-time unstable (July 16, 2002, 14:30–15:00) and night-time stable (July 16, 2002, 02:00–02:30) conditions inside and above forest. Forest height is approximately 14 m

the wind profile (Fig. 5.3.3). In addition, in the vicinity of rough surfaces such as forests a roughness sublayer exists where wind gradient is reduced in comparison to the form of the profile above. The roughness sublayer thickness is between one to two characteristic heights of the rough surface, in case of forests this is the forest height.

During daytime typically unstable conditions prevail which promote turbulence and mixing becomes very efficient. Therefore turbulence tends efficiently to 'smooth' profiles, and gradients of concentrations (and wind speed) are smaller. At night the situation for the temperature is the opposite; radiative cooling at the surface drives the heat flux downward from the atmosphere above and negative temperature gradients occur.

Evapotranspiration of water occurs throughout the canopy during daytime, resulting in higher air water content inside canopy. At night the water transpiration is limited because of stomatal closure, also evaporation from surfaces is typically small, being limited by available energy. Therefore the concentration of water vapor in air is relatively constant with height at night (Fig. 5.3.3).

Clouds

Most clouds are located in the troposphere. Only a few clouds can be found above the troposphere; these include noctilucent and polar stratospheric clouds, which occur in the mesosphere and stratosphere respectively.

Clouds are divided into three general categories according to their outward characteristics: cirrus (denoting "fiber" or "hair"), cumulus (convective clouds) and stratus (layered) clouds. Three major types occur in combination with nimbus denoting the rainy combination of the cloud type. Cloud types are divided into four more

groups that distinguish the cloud's altitude by the cloud base height: High, middle-level, low and in addition vertical clouds, which can have strong up-currents, rise far above their bases and form at many heights.

High clouds, denoted by cirrus, generally form above 5 km, in the cold region of the troposphere. However, in Polar regions, they may form as low as 3 km. At this altitude, water almost always freezes so clouds are composed of ice crystals. The clouds are often transparent. Cirrus clouds do not usually bring precipitation.

Middle-level clouds develop between 2 and 5 km and are denoted by the prefix alto-. They are made of water droplets and are frequently supercooled. The middle-level clouds can bring precipitation in the form of rain or snow; nimbostratus clouds tend to bring constant precipitation and low visibility.

Low clouds are found up to 2 km and include the stratus clouds (dense and grey). From low level clouds stratocumulus clouds often follow a cold front and can produce rain or drizzle. Stratus clouds are layer-like clouds associated with widespread precipitation or ocean air, and often produce drizzle. Cumulus clouds, the fair weather clouds, can also develop into more storm-condition clouds (cumulonimbus, for example), and produce showers, typically in the afternoon.

Clouds affect significantly the short-wave as well as long-wave radiation field in the atmosphere and at the surface. Clouds increase the albedo of the Earth-atmosphere system by scattering the solar radiation and thus have global average short-wave cooling effect of about 50 W m^{-2}. By reducing outgoing long-wave radiation by 30 W m^{-2}, clouds contribute to the greenhouse effect by about 20 W m^{-2} (Wielicki et al., 1995).

5.4 Soil

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5.4.1 Mineral Soil

Soil Textural Classes

Soil denotes the loose upper layer of the Earth's crust covering the solid bedrock. It is a heterogeneous mixture of mineral and organic matter. In the boreal zone, the bedrock is composed mainly of magmatic and metamorphic rocks, such as granite and gneiss. Soils are classified according to particle size into textural classes. Coarser mineral soil particles include silt and sand fractions that are 20–200 μm

and 200–2,000 μm in diameter, respectively. Particles larger than 2,000 μm in diameter are classified as gravel or stones. Coarse particles are composed mainly of such primary silicates as quartz, feldspars and mica, reflecting the mineralogy of parent rocks. The smallest soil particles with <2 μm in diameter are called the clay fraction. Clay particles are dominated by secondary minerals formed by modification of original rock minerals or re-crystallization of their decomposition products during soil formation. These include the secondary layer-silicates called clay minerals as well as hydrous oxides (hydroxyoxides) of Al, Fe and Mn. The oxides are partly poorly crystalline. In contrast to the more or less spherical shape of coarser soil particles, the clay particles are plate-like, reflecting the shape of layer-silicate minerals.

Properties

Soil chemical properties are largely dominated by the reactions occurring at the surfaces of small particles. This is due to the large specific surface area and polar nature of clay minerals and oxides in the smallest particle size fractions. Most clay minerals have a permanent negative electrical charge due to isomorphic substitution of cations within the crystals. These substitutions occur during the crystallization of minerals and remain unchanged thereafter. On the other hand, the oxides may be negative, neutral or positive depending on soil acidity that determines the protonation and deprotonation of their hydroxyl groups. Soils generally have a net negative charge and thus adsorb cations on their surfaces by electrostatic forces and retain anions on the hydroxyl groups of clay mineral edges and oxide surfaces by specific mechanisms. These processes are discussed in more detail later (Section 6.2.4).

Larger Mineral Soil Fragments

Boreal forest soils often contain considerable amounts of gravel and stones. However, these larger fractions are chemically inert and mainly occupy space from more fertile and porous soil composed of finer fractions. In practice, soil texture refers to the size fractions finer than 2 mm in diameter. Moreover, the conventional pretreatments for the determination of particle size distribution include the removal of organic matter and oxides that bind the silicate particles together.

5.4.2 Soil Organic Matter

Definition and Origin of Soil Organic Matter

Soil organic matter denotes all living and dead biologically derived organic material at various stages of decomposition in the soil or on the soil surface, excluding the

above-ground portion of living plants (Baldock and Nelson, 2000). In practice, the concept has often a narrower scope referring to materials passing through a 2-mm sieve (Nelson and Sommers, 1996) excluding undecayed plant and animal residues.

Origin and Molecular Structures of Soil Organic Matter Compounds

Soil organic matter includes all organic compounds entering the soil through the root growth and the litterfall from above-ground plant parts as well as the products of their microbial decomposition and re-synthesis. Microbial decomposition of organic macromolecules produces a range of small molecules as well as the decay-resistant, dark, amorphous organic matter called humus.

The chemical composition of soil organic matter is similar to that of litter unless not changed by microbial decomposition. Biological tissues are composed of various organic macromolecules and a lesser amount of small molecules. The chemical composition of organic residues depends on the tissue (reviewed by Baldock and Nelson, 2000; Derenne and Largeau, 2001; Blume et al., 2002; Kögel-Knabner, 2002). Within the plasma membrane, the cells contain phospholipids, carbohydrates, lignin, nucleic acids and proteins, as well as such smaller molecules as sugars, amino acids and dissolved inorganic ions. The cell walls of plants are composed mainly of cellulose, hemicellulose and lignin. Cellulose is a carbohydrate polymer of 1–4 β-linked glucose units, whereas hemicellulose contains other sugars as well. In contrast, lignin is not a carbohydrate and has a complex structure composed of linked phenyl propane units. The nitrogenous compounds constitute a small but important group, as nitrogen is a structural component of enzymes and other proteins as well as nucleic acids, ATP and such pigments as heme and chlorophyll.

The chemical composition of microbial cells resembles plant cells. However, the cell walls of fungi contain mainly chitin, a polymer of 1–4 β-linked N-acetyl-glucoseamine units, and those of bacteria peptidoglucanes and/or lipopolysaccharides. As a consequence, the composition of soil microbes is dominated by phospholipids and protein-like chemical species. The chemical composition and functional role of biological macromolecules in plant and microbial tissues is discussed in more detail in the preceding chapter.

Humus is traditionally considered to be composed of large molecules with a complex structure not amenable for detailed structural characterization. The classical fractionation of humic substances is based on their acidity-dependent solubility characteristics. The humic substances that are extracted by an alkaline solution and remain soluble after subsequent acidification are fulvic acids, whereas those in the acid-precipitated fraction are humic acids. Still, large amounts of humic substances called humins may remain unextracted by the alkali. Humins are mostly humic acids that have very high molecular weight or are protected by mineral soil particles. The classical fractionation of humus has some practical merits, as it separates the fulvic acids that are soluble and potentially mobile in a broad pH range in soil, in contrast to the humic acids that are immobile in acid conditions. Nevertheless, the molecular structure of humus has long been and still is a topic of active research and discussion

(Schnitzer, 2000; Burdon, 2001; Piccolo, 2001; Sutton and Sposito, 2005). Current views question the macromolecular nature of humus. Instead, the humic substances are best described as collections of diverse, relatively low molecular mass components that form supramolecular associations stabilized by hydrophobic interactions and hydrogen bonds (Sutton and Sposito, 2005).

Humus contains numerous acidic groups that can dissociate in a broad pH range which gives rise to pH-dependent negative charge of soil particles. For this reason, it is the dominant soil constituent responsible for the cation exchange capacity in coarse-textured soils, such as those in boreal forest.

Analysis of Soil Organic Matter

The amount and composition of soil organic matter can be analysed by various methods. The crudest approaches involve the determination of organic matter based on the loss-on-ignition or the organic carbon content. However, the treatment of soil organic matter according to its chemical structure allows efficient use of quantitative methods, since all soil components can, at least in principle, be directly measured. Quantitative data on the different chemical groups of biological macromolecules can be obtained by combinations of selective extractions, such as the proximate methods used in the food chemistry, or more generally, by thermochemolytic degradation of macromolecules followed by compound-specific analysis of the products (see Kögel-Knabner, 2000). Non-destructive spectroscopic methods allow the characterization of various groups of atoms, but the quantification of various molecular groups is not yet reliable (Kögel-Knabner, 2000), although, e.g., Nelson and Baldock (2005) made an attempt to apply a solid-state ^{13}C NMR technique towards this aim.

Traditionally, different empirical wet chemical methods have been used for the analysis of litter and humus. Nonetheless, the strict separation of soil organic matter into litter and humus fractions is not feasible with conventional extractions (Beyer, 1996). For this reason, Beyer et al. (1996) recommended applying litter compound analysis to soil as well. Moreover, application of the same analytical procedures for both plant and soil samples provides methodological advantages.

For the above reasons, we planned and carried out a uniform analytical procedure for the determination of chemical composition of plant tissues, litter and soil organic matter by combining dry and wet chemical methods of food and soil chemistry. The procedure is outlined in Figs. 5.4.1 and 5.4.2 and Box A. The analyses take advantage of the fact that biological macromolecules are composed of specific monomers. This allows the estimation of main organic macromolecules, including (1) lipids, (2) sugars and starch, (3) hemicellulose + cellulose, (4) lignin, and (5) proteins and other nitrogenous compounds. The lignin is determined as undissolved Klason lignin residue. In soil samples, this residue contains humus as well. Nitrogenous organic compounds fall into several fractions (Fig. 5.4.2). For simplicity, however, the protein content in this study was estimated according to the convention of food chemistry as a crude protein by multiplying the content of total hydrolysable N

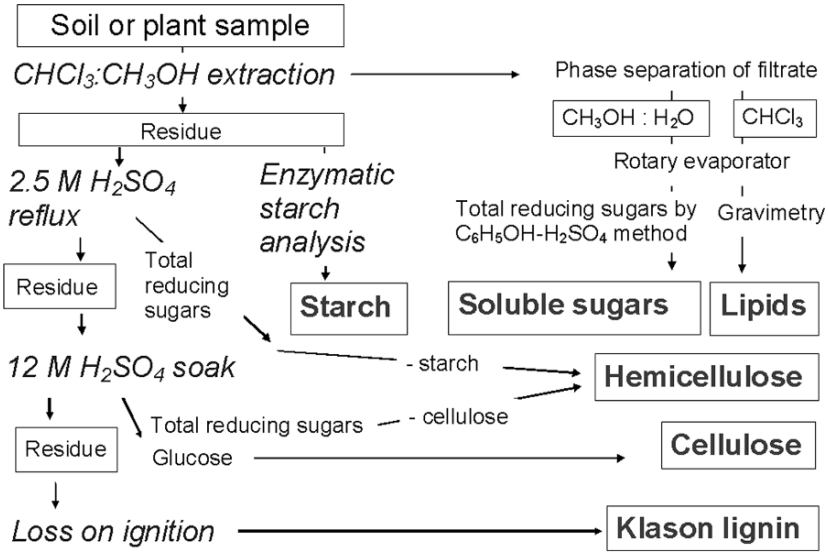

Fig. 5.4.1 Sequential extraction and analysis of various organic fractions of soil and plant by solvent, mild acid and strong acid. Lipid extraction with chloroform:ethanol solution (Bligh and Dyer, 1959; Kögel-Knabler, 1995). Double hydrolysis scheme for polysaccharides (Oades et al., 1970; Swift, 1996). Analysis of total reducing sugars by phenolic sulphuric acid method (Dubois et al., 1956; Wood and Bhat, 1988). Enzymatic analysis of starch by hot gelatinisation and amyloglucosidase (AG) incubation. Analysis of glucose by glucose oxidase peroxidase method (GOP; Karkalas, 1985)

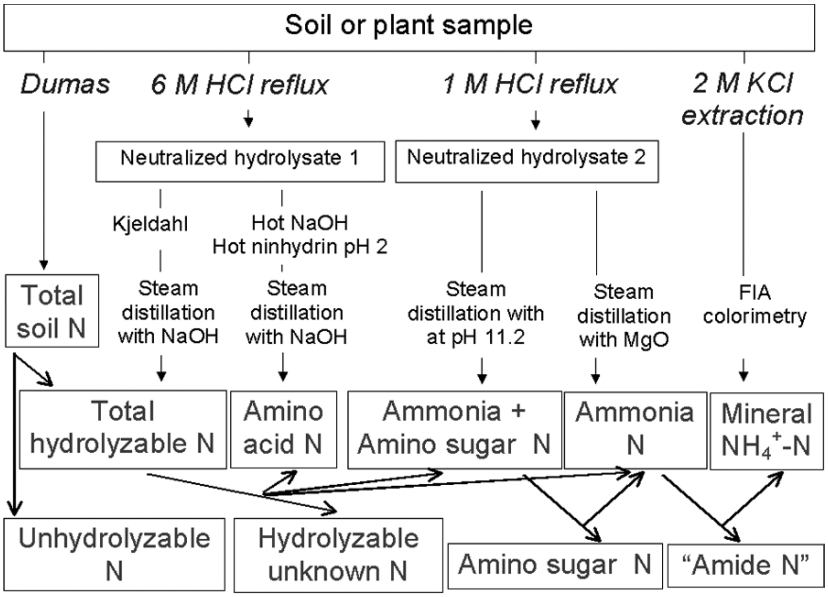

Fig. 5.4.2 Methods for determining the various forms of nitrogen in soil and plant (Bremner, 1965; Yonebashi and Hattori, 1980). Reflux in 70 ml screw-capped Pyrex bottles. Steam distillation with boric acid indicator in the collection flask. Flow injection analysis by QuikChem® 8000 (LACHAT Instruments, QuikChem® method 12-107-06-2-A)

by 6.25 (assuming 16% N in the proteins). "Humus N" was obtained as a difference between the total and hydrolysable N.

Box A

Air-dried and ground/sieved (<2 mm) materials were used for the analyses (soil from O and A horizons, green needles, litter, wood). Lipids, carbohydrates and lignin were determined by sequential extraction with a chloroform-methanol solution and sulphuric acid solutions. Nitrogenous compounds were determined by dry combustion and extraction with neutral salt and hydrochloric acid solutions. The amount of organic matter was determined as loss on ignition (within 2 h to 550°C plus 1 h burning).

Lipids and soluble sugars were extracted by a chloroform-methanol solution (N_2 bubbled samples, 16 h) (Bligh and Dyer, 1959; Kögel-Knabler, 1995). After the phase separation, the chloroform layer was evaporated to dryness by a rotary evaporator and the lipids were determined by gravimetry. The soluble sugars in the methanol-water layer were determined as total reducing sugars by the phenolic-sulphuric acid method (Dubois et al., 1956; Wood and Bhat, 1988). Polysaccharide and Klason lignin fractions were determined from the residue after the chloroform-methanol extraction. Starch was determined enzymatically by hot gelatinisation and amyloglucosidase (AG) incubation. Glucose was analysed by the glucose oxidase peroxidase method (GOP, Karkalas, 1985) and converted to starch ($\times 0.9$). A double-hydrolysis scheme with 2.5 M H_2SO_4 (reflux, 20 min) and 12 M H_2SO_4 (soak 20°C, 16 h) was used for polysaccharides (Oades et al., 1970; Swift, 1996). Cellulose was determined by the amount of glucose ($\times 0.9$) in the 12 M H_2SO_4 extract. Hemicellulose was determined by the sum of the amount of total reducing sugars ($\times 0.9$) in the 2.5 M H_2SO_4 and 12 M H_2SO_4 extracts (phenolic-sulphuric acid method) minus the contributions due to starch and cellulose in the extracts, respectively. The amount of Klason lignin was determined by the loss on ignition of the residue after 12 M H_2SO_4 extraction. This was done at 400°C for 16 h (Nelson and Sommers, 1996), as the glass fibre filters (Whatman GC/C) were not stable at higher temperatures. In soil samples, the Klason lignin fraction includes also humus compounds (humic acids and humin).

Total N content was determined by dry combustion (Leco® CSN-analyser). Fractions of organic nitrogen were determined by the extraction with 6 M and 1 M hydrochloric acid solutions and steam distillation techniques (Stevenson, 1996; Yonebashi and Hattori, 1980). Neutralised hydrolysates were steam distillated and titrated with Kjeltec Auto 1030 Analyzer (macro-Kjeldahl tubes, 40 ml hydrolysate, boric acid indicator, 0.025 M H_2SO_4). Total acid hydrolysable N was determined by the extraction with 6 M HCl (reflux in capped pyrex bottles, 110°C, 24 h, Salo-Väänänen, 1996). Half of the hydrolysate was analysed for the total hydrolysable N by Kjeldahl digestion and steam distillation with NaOH. For the determination of amino acid N in the other half of the hydrolysate, the hydrolysate was pretreated with hot

NaOH (100°C, 20 min) to remove amino sugars plus hot ninhydrin (pH 2, 100°C, 10 min) to convert α-amino-N to ammonium ions, and then steam distillated with NaOH. Amino sugars and ammonium N were determined by extraction with 1 M HCl (reflux, 3 h). Half of the hydrolysate was steam distillated with a phosphate-borate buffer (pH 11.2) to give the sum of amino sugars and ammonium N. The contribution of ammonium was estimated from the other half by steam distillating it with MgO. The amount of mineral ammonium was small, as estimated by the extraction of samples with 2 M KCl (10 g sample, 100 ml solution, 1 h) and colorimetric analysis of ammonium by flow injection analysis (Lachat Instruments QuikChem® 8000, QuikChem® method 12-107-056-2-A).

5.4.3 Soil Structure, Water and Air

Forest soil is a mixture consisting of soil particles, water and air. Soil structure generally denotes the spatial arrangement of soil particles and pore space between them. Natural structural development of soil involves spatial heterogenization of soil. In fine-textured soils that contain much clay, the individual mineral and organic particles are clustered together into larger units called aggregates or peds of various shapes and sizes. The aggregates in soils containing even modest amounts of organic matter show a hierarchical structure (Tisdall and Oades, 1982; Oades, 1993): the particles form microaggregates that are joined together into macroaggregates. Clay, humus and oxides often coat the coarse particles and aggregate surfaces. This kind of secondary soil structure is not well developed in boreal forest soils that are mostly coarse in texture. The structure of coarse-textured soils is predominantly single-grained, with roots, fungal hyphae, organic biopolymers and oxides providing only limited binding of particles together. However, the channels of old plant roots and earthworms or other burrowing animals often provide a stable system of continuous large pores in both fine and coarse textured soils (Lee and Foster, 1991; Oades, 1993; Angers and Caron, 1998).

The pore space between soil particles or aggregates is filled with water or air and is a site for chemical reactions and a habitat for soil organisms. Most reactions and microbial activity occur in the water-filled pore space. The facts that soil particles have charged surfaces and that water molecules are permanent dipoles, i.e. water molecules have electrically positive and negative areas, explain the behaviour of water in the soil (Hillel, 1998). Electric forces bind the water molecules to particle surfaces and with each other. Water forms layers on soil particles in which the first layer of water molecules are bound electrically to the particle surface (adhesion) and thereafter the water molecules are bound electrically with each other (cohesion).

At the border (interface) between water and air, the neighboring water molecules interact with each other unequally at different directions, as the molecules inside the

water phase pull the molecules from the surface inwards, while the pull towards the air phase is negligible (Hillel, 1998). This net inward force causes a flow of water molecules from the surface deeper into the water until an equilibrium is reached at which the electric forces in the interface between water and air are strong enough to resist further flow and the surface area of water is minimized. As a result, the water molecules at the interface are bound electrically more strongly with each other than with the molecules of bulk water, and form a clear film (meniscus) separating the water and air phases. The film acts like an elastic membrane between water and air phases resisting any forces that tend to increase its surface area. The magnitude of phenomenon is quantified by the coefficient of surface tension (unit $\mathrm{N\,m^{-1}}$), or equivalently by the coefficient of surface energy (unit $\mathrm{J\,m^{-2}}$).

The shape of water-air interface at equilibrium with external forces neglecting gravity satisfies the Young-Laplace equation.

$$\Delta P = \gamma\left(\frac{1}{r_1} + \frac{1}{r_2}\right) \tag{5.4.1}$$

or

$$\Delta P = \gamma\frac{2}{r}, \text{with } r = \frac{2\,r_1\,r_2}{r_1 + r_2} \tag{5.4.2}$$

where ΔP ($= P_{water} - P_{air}$) is the pressure difference across the water-air interfacial membrane, γ the coefficient of surface tension, r the equivalent radius of curvature of the surface, and r_1 and r_2 the radii of curvature lying in planes normal to each other at a point on the interface as shown in Fig. 5.4.3 (Adamson and Gast, 1997; Hillel, 1998). The radius of curvature r is taken as positive, if the radius lies within water (such as r_1 in Fig. 5.4.3). In words, these equations state that at equilibrium the soil water-air interfaces are characterized by a uniform curvature that may be produced by innumerous combinations of radii of curvature. The radius of curvature is determined by the boundary conditions determined by the contact angle (α) of water with the solid phase and the pore size (for a hemispherical surface $r = R/cos\ \alpha$, where R is the equivalent pore radius). The contact angle is commonly taken as zero for soil minerals, indicating a completely wetting surface, although in reality it depends on the relative magnitudes of interfacial surface energies between solid, liquid and gas phases. However, humic coatings on dry soil mineral particles may increase the contact angle up to hydrophobism ($>90°$). In wet soil, water-repellency is less pronounced. Bachmann and van der Ploeg (2002) reviewed the recent developments in interfacial tension and temperature effects on soil water retention.

According to the Young-Laplace equation, no pressure difference exists across the flat surface of free water. In unsaturated soils, however, the water molecules generally adhere to the solid particles. Owing to high surface tension of water, this produces concavely curved water-air interfaces with contact angles $<90°$ with the solid phase, which decrease the pressure in soil water below that in soil air. In such a case, soil water is under tension (underpressure, suction), the magnitude of which gives the strength of water retention in the capillary pores of soil (unit Pa or $\mathrm{J\,m^{-3}}$).

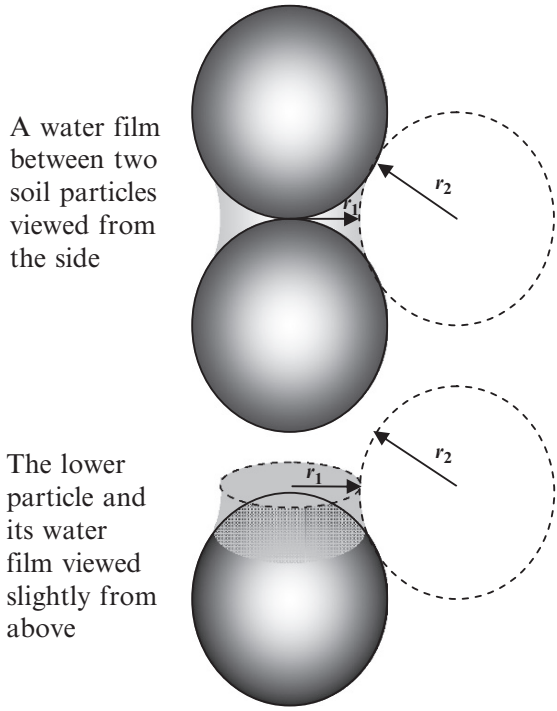

Fig. 5.4.3 Two radii of curvature (r_1 and r_2) in planes normal to each other in a pendular water between two spherical soil particles

The phenomenon of capillarity explains, why the largest pores empty first in a drying soil, while the smaller pores remain filled with water, because the curvature of water film and the resulting pressure difference increase (the radius of curvature decreases) with decreasing pore size. Small-sized humus is thus important in increasing the retention of water in coarse textured soils. Capillarity is also important, as the pressure difference between water and air phase drives water flux from lower to higher tension, and cause capillary rise from the free ground water table upwards into drier soil until the capillary forces are balanced by the gravity (the weight of water column).

Besides water, soil solution contains small amounts of organic and inorganic dissolved species. They typically decrease the surface tension of soil solution only slightly below that in pure water and thus have minor influence on the retention of water in soil.

In contrast to the small pores mostly filled with water, larger soil pores drain out quickly and are air-filled for most of the time. Soil air is in essence atmospheric air nearly saturated with water vapour and continuously modified by consumption and production of gases in soil. The amount, shape and distribution of air-filled pores is determined in a complementary manner by soil solid and liquid phases. Soil structure is thus an important determinant of soil functions, as it ultimately

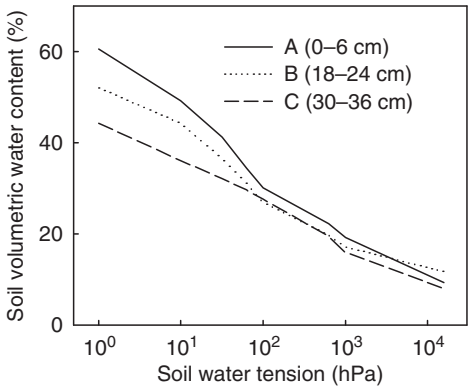

Fig. 5.4.4 Soil water retention curves at various depths of mineral soil horizons in a podzol soil at the SMEAR II station

determines the retention (Fig. 5.4.4) and flux rates of water, nutrients and gases supporting the processes that change material from one form to another in the soil.

5.4.4 Soil Organisms

Besides plant roots, numerous organisms live in the soil. The primary function of soil organisms in the soil ecosystem is the processing and mixing of soil organic matter (Killham, 1994). They can be classified according to size into microflora (archae, bacteria, fungi), micro- and mesofauna (e.g., protozoa, rotifers, tardigrades) and macrofauna (e.g., nematodes, earthworms, Enthytraeidae, arthropods) (see e.g., Blume et al., 2002). The microfauna (less than 100 μm in dimension), also called protozoa, consists of flagellates, ciliates, amoebae and sporozoa (Paul and Clark, 1989; Killham, 1994). Protozoa live mainly by grazing soil microbes, bacteria and fungi. The most important members of larger soil fauna, meso- (from 100 μm to 1–2 mm) and macrofauna (greater than 1–2 mm) are the earthworms, enchytraeid worms, nematodes, arthropods (e.g. mites and Collembola), molluscs and mammals. Macrofauna can move quite freely in soil pore space, and the largest ones can even burrow their own channels through the soil. On the contrary, the smaller organisms can not move around in the soil and are limited to the small water-filled pores and films covering the soil particles to prevent dehydration by drying and predation by soil animals.

The largest amounts of soil organisms live in the immediate vicinity of roots (rhizosphere) and in soil surface layers containing ample decomposable organic compounds. Some bacteria and fungi live even within plant roots, such as the symbiotic nitrogen-fixing bacteria and mycorrhiza (Fig. 5.2.10). Moreover, a part of the soil microbiota belongs to the phyla *Archaea*. It was earlier thought that *Archaea* can only grow under very extreme conditions (in high salinity, or in high temperature, or in anaerobic conditions), but it has been shown that *Archaea* exist also in great numbers in acid boreal forest soils (Jurgens et al., 1997).

5.4.5 Soil Horizons and Distribution

The soil covering the Earth surface is not similar everywhere; its composition, structure and properties vary in space. Such differences appear on a global scale and in different vegetation zones as well as within landscapes and individual soil profiles. The differences originate partly from the transport and sedimentation of parent material, and partly from the gradual processes of local soil formation. As a consequence, dominant soil texture differs in different geographical areas, and the surface layers of a well-developed soil profile show distinct horizons differing in colour, chemical properties, or structure.

Boreal forest soils are mostly coarse-textured for several reasons. In the boreal zone, much of the soil parent material originates from the Holocene ice age. During and after deglaciation, much of the fine soil material was transported to more southern latitudes by melting waters, whereas the coarser material remained in place (see e.g. Salminen, 2005). Within the boreal zone, the finer soil fractions have been deposited at the bottom of lakes and seas, whereas the supra-aquatic soils at higher elevations are coarse-textured glacial till. As the land level rose after deglaciation, the lake and sea sediments partly mixed with coarser coastal sediments and became eventually dry land. Later, the fine-textured soils were preferred for agricultural land use rather than forestry due to their fertility.

Soil organic matter accumulates near the soil surface. This may even form an organic surface horizon (litter or humus layer) above the mineral soil. Deeper in the soil, humus covers larger mineral soil particles and forms complexes with clay particles.

In humid climates such as in the boreal zone, coarse-textured forest soils typically have a podsolic profile. It is characterized by an acidic litter and humus layer underlain by a dark-coloured mineral soil horizon, a greyish eluviation horizon and a reddish dark brown illuviation horizon. The bottom of the profile is practically unchanged parent material. Podsol soils are most common under boreal forests (see Section 7.4).