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Ministry of Higher Education and Scientific Research
University of Bejaia
Faculty of Natural and Life Sciences
Department of Environment Biological Sciences

Plant physiology

(Physiologie végétale)

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Table of contents

Part 1. Nutrition and metabolism

Part 2. Growth and development

Preface

Within the *planta* world, green plants constitute the largest group, with around 278,000 different species. The four main subdivisions of the green plant group are mosses, ferns, conifers and flowering plants. The latter are so far the most represented, with nearly 234,000 species. Mushrooms are traditionally presented alongside plants although they are not part of them. They form a distinct, homogeneous group, made up of species that obtain their food from other organisms. Algae, for their part, do not all come from the same ancestor and make up a heterogeneous group. Brown algae form a separate group, while red and green algae are part of plants.

Plants serve as a source for sustainable food and biofuel and also play crucial roles in maintaining human health and ecosystem. Thus, it becomes imperative to understand the mechanisms of plant growth and development. Plant physiology is that significant branch of plant science which deals with understanding the process of functioning of plants at cell, molecular, and whole plant levels and their interaction with the surrounding environment. In spite of being static in nature, plants can withstand adverse growth conditions due to a variety of adaptive mechanisms. Intracellular compartmentalization of biochemical pathways, expression of membrane-associated transporter proteins specific for various ions and metabolites, production of secondary metabolites with multiplicity of protective functions, and a wide variety of photoreceptors biochemically synchronized with various environmental and developmental conditions are some of the noteworthy adaptive features of plants enabling them to survive in almost all possible situations. The plethora of information available today has been made possible through interaction of cell and molecular biology, biochemistry, and genetics to understand plant processes.

Plant physiology is an experimental science. Plant water relation is the first area of research in plant physiology which caught attention of scientists. Stephen Hales, also called as the Father of Plant Physiology, published the book Vegetable Staticks in 1727, highlighting various experimental studies on transpiration and root pressure. In the beginning of twentieth century, the development of physicochemical and biochemical techniques further facilitated the understanding of the plant processes. These techniques include spectral analysis, mass spectrometry, differential centrifugation, chromatography, electrophoresis, and the use of radioisotopes, besides many others. In the last two decades, plant physiologists made an extensive use of the molecular tools and Arabidopsis as a model organism to facilitate learning about the role of genes and the crosstalk among various biomolecules affecting plant functions and development.

Students continue to ponder the age-old questions of – what will I do in my life ahead, how can I make a difference with my profession or vocation, and how can I, we, make our planet a better place? Such questions move to answer – through knowledge, understanding, a belief in evidence, a passion for ‘place’, and then participating in doing plant physiological (PP). PP is a hub around which the plant world and the Earth revolve. This work serves as a valuable source of acknowledge for undergraduate students that pursuing their formation in the fields of Ecology and Environment, Food Science and Agronomy.

This manuscript is split up into two parts (Nutrition and Development). The uptake and transport of water and minerals are explained in general. Most common processes of plant biochemistry and metabolism, such as photosynthesis, are highlighted. The nutrient supply of plant is presented in details (essential elements and solute transport). Plant growth and development is introduced with the characterization of plant growth approaches.

Part 1. Nutrition and metabolism

Chapter I. Water plant nutrition

1. Water in plant life

Water plays a crucial role in the life of plant. It is the most abundant constituents of most organisms. Water typically accounts for more than 70 percent by weight of non-woody plant parts. The water content of plants is in a continual state of flux. The constant flow of water through plants is a matter of considerable significance to their growth and survival. The uptake of water by cells generates a pressure known as turgor. Photosynthesis requires that plants draw carbon dioxide (CO_2) from the atmosphere, and at the same time exposes them to water loss. To prevent leaf desiccation, water must be absorbed by the roots, and transported through the plant body. Balancing the uptake, transport, and loss of water represents an important challenge for terrestrial plants. The thermal properties of water contribute to temperature regulation, helping to ensure that plants do not cool down or heat up too rapidly. Water has excellent solvent properties. Many of the biochemical reactions occur in water and water is itself either a reactant or a product in a large number of those reactions. The practice of crop irrigation reflects the fact that water is a key resource limiting agricultural productivity. Water availability likewise limits the productivity of natural ecosystems (**Figure 1**). Plants use water in huge amounts, but only small part of that remains in the plant to supply growth. About 97% of water taken up by plants is lost to the atmosphere, 2% is used for volume increase or cell expansion, and 1% for metabolic processes, predominantly photosynthesis. Water loss to the atmosphere appears to be an inevitable consequence of carrying out photosynthesis. The uptake of CO_2 is coupled to the loss of water (**Figure 2**). Because the driving gradient for water loss from leaves is much larger than that for CO_2 uptake, as many as 400 water molecules are lost for every CO_2 molecule gained.

2. Water potential

The structure and properties of water

Water consists of an oxygen atom covalently bonded to two hydrogen atoms (**Figure 3**). The oxygen atom carries a partial negative charge, and a corresponding partial positive charge is shared between the two hydrogen atoms. This asymmetric electron distribution makes water a **polar molecule**. However, the partial charges are equal, and the water remains a neutral molecule. There is a strong electrical attraction between adjacent water molecules or between water and other polar molecules, which is called hydrogen bonding. The **hydrogen bonding** ability of water and its polar structure make it a particularly good solvent for ionic substances and for molecules such as sugars and proteins. The hydration shells that form around biologically important macromolecules are often referred to as **bound water**. Bound water prevents protein molecules from approaching close enough to form aggregates large enough to precipitate.

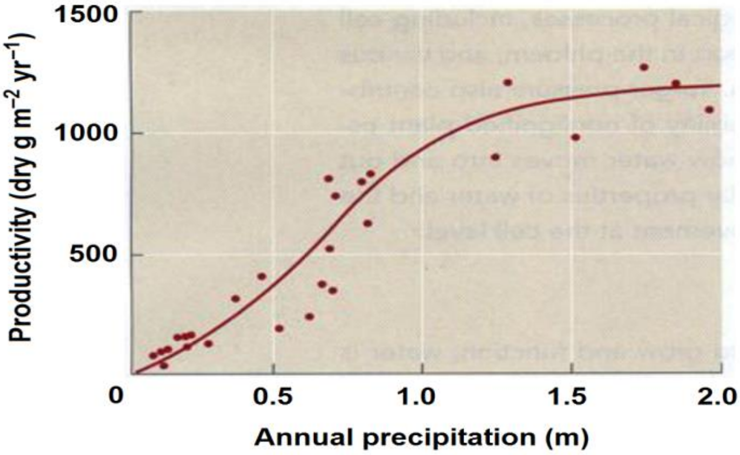


Figure 1 Productivity of various ecosystems as a function of annual precipitation.

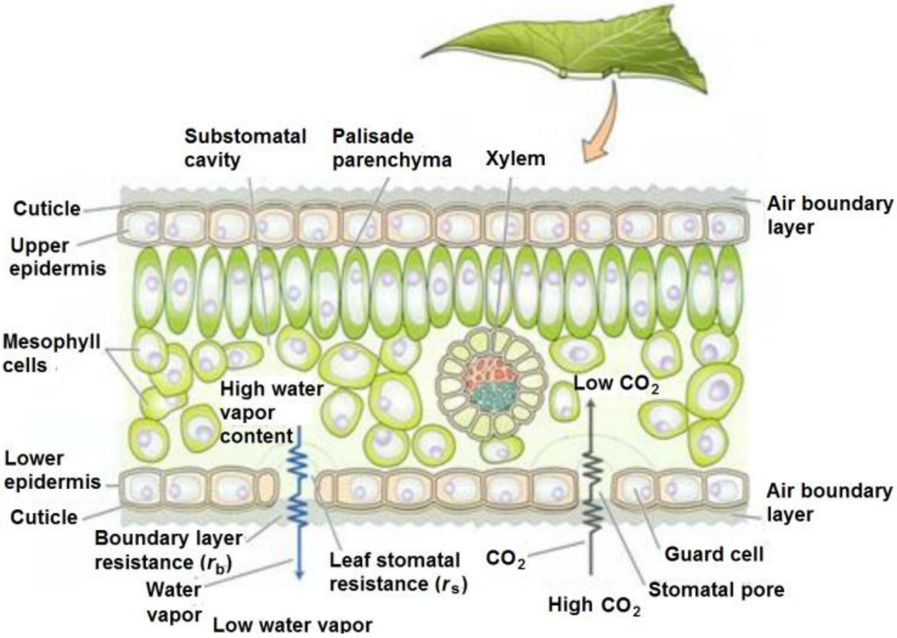


Figure 2 Water pathways through the leaf.

The extensive hydrogen bonding between water molecules results in water having both a high **specific heat capacity** and a high **latent heat of vaporization**. Because of its highly ordered structure, liquid water also has a high **thermal conductivity**. This means that it rapidly conducts heat away from the point of application. The combination of high specific heat and thermal conductivity enables water to absorb and redistribute large amounts of heat energy without correspondingly large increases in temperature. The heat of biochemical reactions may be quickly dissipated throughout the cell. Compared with other liquids, water requires a relatively large heat input to raise its temperature. This is important for plants, because it helps buffer temperature fluctuations. The latent heat of vaporization decreases as temperature increases, reaching a minimum at the boiling point (100°C). For water at 25°C, the heat of vaporization is 44 kJ mol^{-1} (i.e., the highest value known for any liquid).

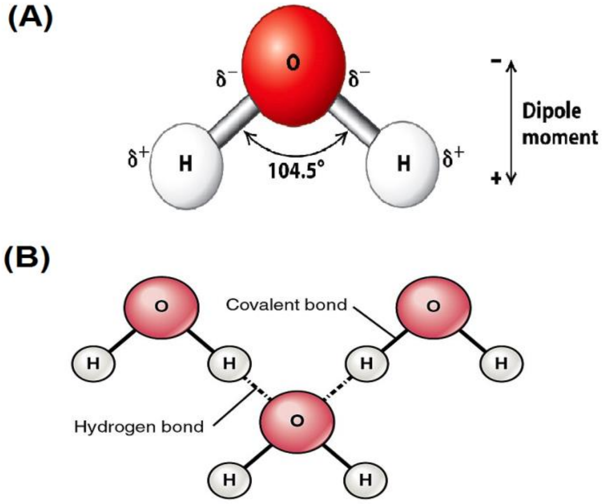


Figure 3 A) Structure of a water molecule. B) Hydrogen bonds among water molecules

The extensive hydrogen bonding in water gives a new property known as **cohesion**, the mutual attraction between molecules. A related property, called **adhesion**, is the attraction of water to a solid phase, such as cell wall. The water molecules are highly cohesive. One consequence of cohesion is that water has exceptionally high **surface tension**, which is the energy required to increase the surface area of a gas-liquid interface. Surface tension and adhesion at the evaporative surfaces in leaves generate the physical forces that pull water through the plant's vascular system. Cohesion, adhesion and surface tension give rise to a phenomenon known as **capillarity**. These combined properties of water help to explain why water rises in capillary tubes and are exceptionally important in maintaining the continuity of water columns in plants.

Hydrogen bonding gives water a high tensile strength, defined as the maximum force per unit area that a continuous column of water can withstand before breaking. Water can resist pressures more negative than –20 MPa, where the negative sign indicates tension, as opposed to compression. Pressure is measured in units called pascals (Pa), or more conveniently, megapascals (MPa). One MPa equals approximately 9.9 atmospheres.

Water movement by diffusion, osmosis and bulk flow

Movement of substances from one region to another is commonly referred to as translocation. Mechanisms for translocation may be classified as either active or passive. It is sometimes difficult to distinguish between active and passive transport, but the translocation of water is clearly a passive process. Passive movement of most substances can be accounted for by **bulk flow** or **diffusion**. The diffusion of water across a selectively permeable barrier is known as **osmosis**, which must also be taken into account.

The molecules in a solution are not static, they are in continuous motion. Diffusion results in the net movement of molecules from regions of high concentration to regions of low concentration. This tendency for a system to evolve toward and even distribution of molecules can be understood as a consequence of the second law of thermodynamics, which tells us that spontaneous processes evolve in the direction of increasing entropy or disorder. Diffusion represents the natural tendency of systems to move toward the lowest possible energy state. Fick’s first law describes the process of diffusion, which is most effective over short distances. Diffusion in solutions can be effective within cellular dimensions but is far too slow to be effective over long distances. The average time required for a glucose molecule to diffuse across a cell with a diameter of 50 μm is 2.5 s. However, the average time needed for the same glucose molecule to diffuse a distance of 1 m in water is approximately 32 years.

The net movement of water across a selectively permeable barrier is referred to as osmosis. Membranes of plant cells are selectively permeable. The diffusion of water directly across the lipid bilayer is facilitated by **aquaporins**, which are integral membrane proteins that form water-selective channels across membrane. In osmosis the maximization of entropy is realized by the volume of solvent diffusing through the membrane to dilute the solute. Osmosis can be easily demonstrated using a device known as an osmometer, constructed by closing off the open end of a thistle tube with a selectively permeable membrane (**Figure 4**). If the tube is filled with a sugar solution and inverted in a volume of pure water, the volume of solution in the tube will increase over time. The increase in the volume of the solution will continue until the hydrostatic pressure developed in the tube is sufficient to balance the force driving the water into the solution.

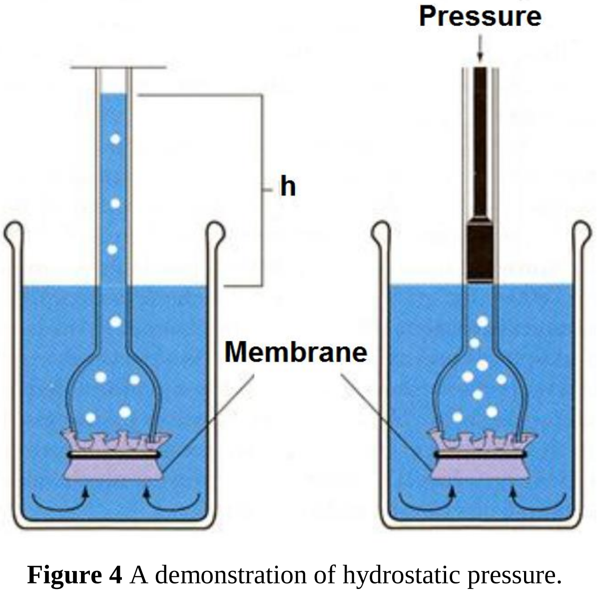


Figure 4 A demonstration of hydrostatic pressure.

The concept of water potential

All living things, including plants, require a continuous input of free energy to maintain and repair their highly organised structures, as well as to grow and reproduce. Chemical potential is a quantitative expression of the free energy associated with a substance. The chemical potential of the water represents the free energy associated with water. Water flows without energy input from regions of higher chemical potential to ones of lower chemical potential. The concept of water potential was introduced in 1960 by R.O. Slatyer and S.A. Taylor, as a measure of the free energy of water per unit volume ($J.m^{-3}$). These units are equivalent to pressure units such as the pascal, which is the common measurement unit for water potential.

The major factors influencing the water potential in plants are *concentration, pressure and gravity*. Water potential is symbolized by Ψw (the Greek letter psi), and the water potential of solutions may be dissected into individual components, usually written as the following sum:

$\Psi w = \Psi s + \Psi p + \Psi g$

The terms Ψs, Ψp and Ψg denote the effects of solutes, pressure, and gravity, respectively, on the free energy of water. The reference state most often used to define water potential is pure water at ambient temperature and standard atmospheric pressure.

Water potentials can be measured by different methods, among others by the Sholander's pressure chamber (**Figure 5**). In this technique, the organ to be measured is excised from the plant and is partly sealed in a pressure chamber. Before excision, the water column in the xylem is under tension. When the water column is broken by excision of the organ (i.e., its tension is relieved allowing its Ψp to rise to zero), water is pulled rapidly from the xylem into the surrounding living cells by osmosis. The cut surface consequently appears dull and dry.

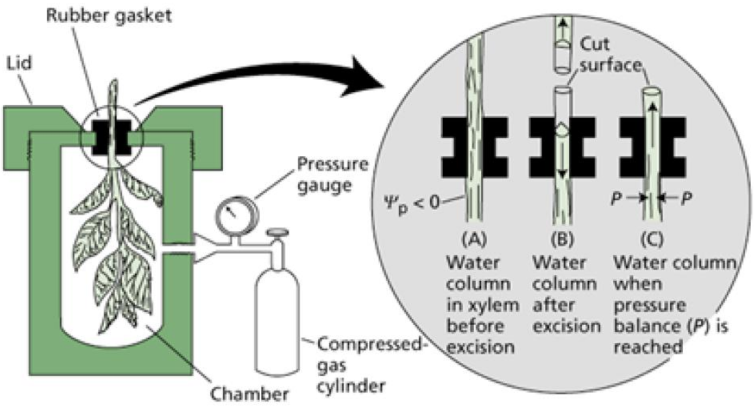


Figure 5 The pressure chamber method for measuring plant water potential.

3. Water absorption

3.1. Water in the soil

The water content and the rate of water movement in soils depend to a large extent on soil type and soil structure. Like the water potential of the plant cells, the water potential of soils may be dissected into three components: the osmotic potential, the hydrostatic pressure and the gravitational potential.

The osmotic potential (Ψs) of soil water is generally negligible. The second component of soil water potential is hydrostatic pressure (Ψp). For wet soils, Ψp is very close to zero. As soil dries out Ψp decreases and can become quite negative. As the water content of the soil decreases, the water recedes into the interstices between soil particles, forming air-water surfaces whose curvature represents the balance between the tendency to minimize the surface area of the air-water interface and the attraction of the water for the soil particles. Water under a curved surface develops a negative pressure (like in leaf mesophyll). As soil dries out, water is first removed from the largest spaces between soil particles. The value of Ψp may easily reach –1 to –2 MPa as the air-water interface recedes into the smaller spaces between clay particles. The third component is gravitational potential (Ψg). Gravity plays an important role in drainage.

3.2. Water absorption by roots

Intimate contact between the surface of root and the soil is essential for effective water absorption. **Root hairs** are filamentous outgrowths of root epidermal cells that greatly increase the surface area of the root, thus providing greater capacity for absorption of ions and water from the soil (**Figure 6**). Water enters the root most readily near the root tip. The intimate contact between the soil and the root surface is easily ruptured when the soil is disturbed. It is for this reason that newly transplanted seedlings and plants need to be protected from water loss for the first few days after transplantation.

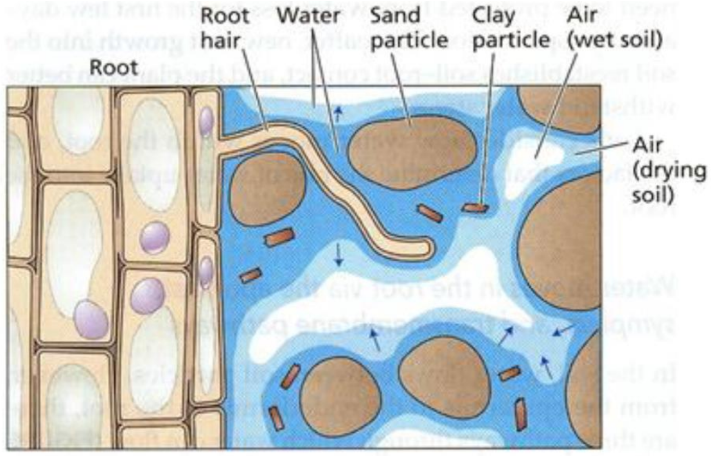


Figure 6 Root hair intimate contacts with soil particles and greatly amplify the surface area used for water absorption by the plant.

From the epidermis to the endodermis of the root, there are three pathways through which water can flow: the apoplast, the symplast and the transmembrane pathway (**Figure 7**).

1. The apoplast is the continuous system of cell walls and intercellular air spaces. In this pathway water moves without crossing any membranes as it travels across the root cortex.

2. The symplast consists of the entire network of cell cytoplasm interconnected by plasmodesmata. In this pathway, water travels across the root cortex via the plasmodesmata.

3. The transmembrane pathway is the route by which water enters a cell on one side, exits the cell on the other side, enters the next in the series, and so on. In this pathway, water crosses the plasma membrane of each cell in its path twice.

Though there are three pathways, water moves not according to a single chosen path, but wherever the gradients and resistances direct it. At the endodermis the Casparian strip breaks the continuity of the apoplast pathway, forcing water and solutes to pass through the plasma membrane in order to cross the endodermis. The requirement that water move symplastically across the endodermis aids explain why the permeability of roots to water depends strongly on the presence of aquaporins.

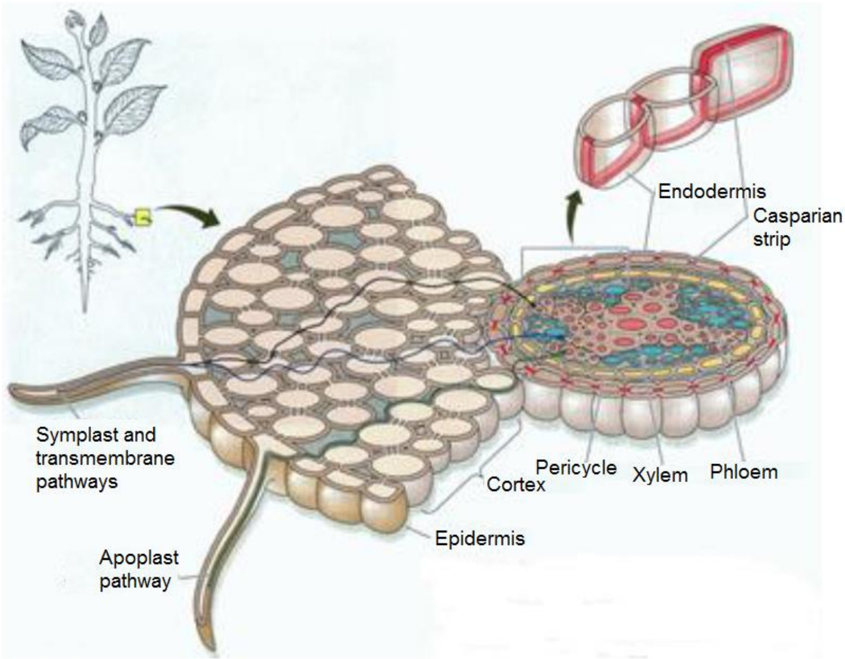


Figure 7 Pathways (symplast, transmembrane and apoplast) for water uptake by the root.

4. Transport of water through the xylem

Vascular tissues include the xylem and phloem, which conduct water and nutrients between the various organs. Xylem tissue is responsible for the transport of water and dissolved minerals from the root to the stem to aerial organs. Phloem, on the other hand, is responsible primarily for the translocation of organic materials from sites of synthesis to storage sites or sites of metabolic demand.

Transpiration speeds up the movement of xylem sap, but it seems unlikely that this is an essential requirement. Transpiration involves the evaporation of water, it can assume a significant role in the cooling of leaves.

The xylem consists of two types of tracheary elements

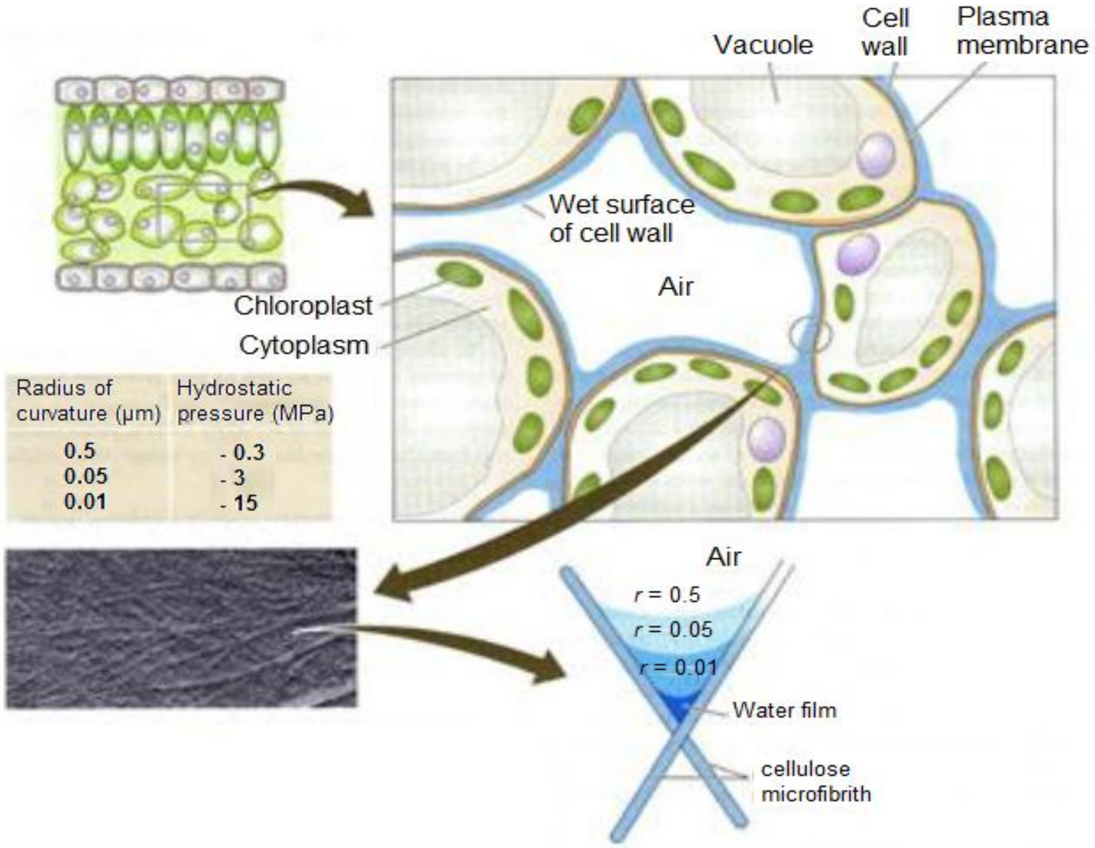
There are two main types of **tracheary elements** in the xylem: tracheids and vessel elements. Vessel elements are found in angiosperms. Tracheids are present in both angiosperms and gymnosperms. Both tracheids and vessel elements dead cells with thick, lignified cell walls, which form hollow tubes through which water can flow with relatively little resistance. **Tracheids** are elongated, spindle-shaped cells that are arranged in overlapping vertical files. **Vessel elements** tend to be shorter and wider than tracheids and have perforated end walls that form a perforation plate at each end of the cell.

Water moves through the xylem by pressure-driven bulk flow

Pressure-driven bulk flow of water is responsible for long-distance transport of water in the xylem. It is independent of solute concentration gradient, as long as viscosity changes are negligible. It is extremely sensitive to the radius of the tube. If the radius is doubled, the volume of flow rate increases by a factor of 16. Vessel elements up to 500 μm in diameter possess nearly an order of magnitude greater than the largest tracheids.

The cohesion-tension theory explains water transport in the xylem

In theory, the pressure gradients needed to move water through the xylem could result from the generation of positive pressures at the base of the plant or negative pressures at the top of the plant. However, root pressure is typically less than 0.1 MPa and disappears when the transpiration rate is high or when soils are dry, so it is clearly inadequate to move water up a tall tree. Instead, the water at the top of a tree develops a large tension (negative hydrostatic pressure), and this tension pulls water through the xylem (**Figure 8**). This mechanism, first proposed toward the end of the nineteenth century, is called the cohesion-tension theory of sap ascent because it requires the cohesive properties of water to sustain large tensions in the xylem water column. The theory is generally credited to H.H. Dixon, who gave the first detailed account of it in 1914.



Radius of curvature (μm)	Hydrostatic pressure (MPa)
0.5	- 0.3
0.05	- 3
0.01	- 15

Figure 8 The driving force for water movement through plants originates in leaves.

The negative pressure that causes water to move up through the xylem develops at the surface of the cell walls in the leaf. As water evaporates from mesophyll cells within the leaf, the surface of the remaining water is drawn into the interstices of the cell wall, where it forms curved air interfaces. Because of the high surface tension of water, the curvature of these interfaces induces a tension, or negative pressure, in water. The cohesion-tension theory explains how the substantial movement of water through plants occurs without the direct expenditure of metabolic energy.

5. **Transpiration**

Water movement is determined by differences in water potential. It can be assumed that the driving force for transpiration is the difference in water potential between the substomatal air space and the external atmosphere. However, because the problem is now concerned with the diffusion of water vapour rather than liquid water, it will be more convenient to think in terms of vapour systems. We can say that when a gas phase has reached equilibrium and is saturated with water vapour, the system will have achieved its **saturation vapour pressure**. The vapour pressure over a solution at atmospheric pressure is influenced by solute concentration and mainly by temperature. In principle, we can assume that the substomatal air space of leaf is normally saturated or very nearly saturated with water vapour. On the other hand, the atmosphere that surrounds the leaf is usually unsaturated and may often have very low water content. This difference in water vapour pressure between the internal air spaces of the leaf and the surrounding air is the driving force of transpiration. On its way from the leaf to the atmosphere, water is pulled from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces of the leaf. The water vapour than exits the leaf through the stomatal pore.

The movement of liquid water through the living tissues of the leaf is controlled by gradients in water potential. However, transport in the vapour phase is by diffusion, so the final part of the transpiration stream is controlled by the concentration gradient of water vapor. Almost all of the water lost from leaves is lost by diffusion of water vapour through the tiny stomatal pores. The stomatal transpiration accounts for 90 to 95% of water loss from leaves. The remaining 5 to 10% is accounted for by cuticular transpiration.

Stomatal control couples leaf transpiration to leaf photosynthesis

Because the cuticle covering the leaf is nearly impermeable to water, most leaf transpiration results from the diffusion of water vapour through the stomatal pore. The microscopic stomatal pores provide a low-resistance pathway for diffusional movement of gases across the epidermis and cuticle. Changes in stomatal resistance are important for the regulation of water loss by the plant and for controlling the rate of carbon dioxide uptake necessary for sustained CO_2 fixation during photosynthesis. At night, when there is no photosynthesis and thus no demand for CO_2 inside the leaf, stomatal apertures are kept small or closed, preventing unnecessary loss of water. Leaf can regulate its stomatal resistance by opening and closing of the stomatal pore. This biological control is exerted by a pair of specialized epidermal cells, the **guard cells**, which surround the stomatal pore.

The cell walls of guard cells have specialized features

Guard cells are found in leaves of all vascular plants. In grasses, guard cells have a characteristic dumpbell shape, with bulbous ends (**Figure 9**). These guard cells are always flanked by a pair of differentiated epidermal cells called **subsidiary cells**, which help the guard cells control the stomatal pores. In dicots and nongrass monocots, guard cells have an elliptical contour (often called "kidney-shaped") with the pore at their center. Subsidiary cells are often absent, the guard cells are surrounded by ordinary epidermal cells. A distinctive feature of guard cells is the specialized structure of their walls. The alignment of cellulose microfibrils, which reinforce all plant cell walls and are an important determinant of cell shape, play an essential role in the opening and closing of the stomatal pore.

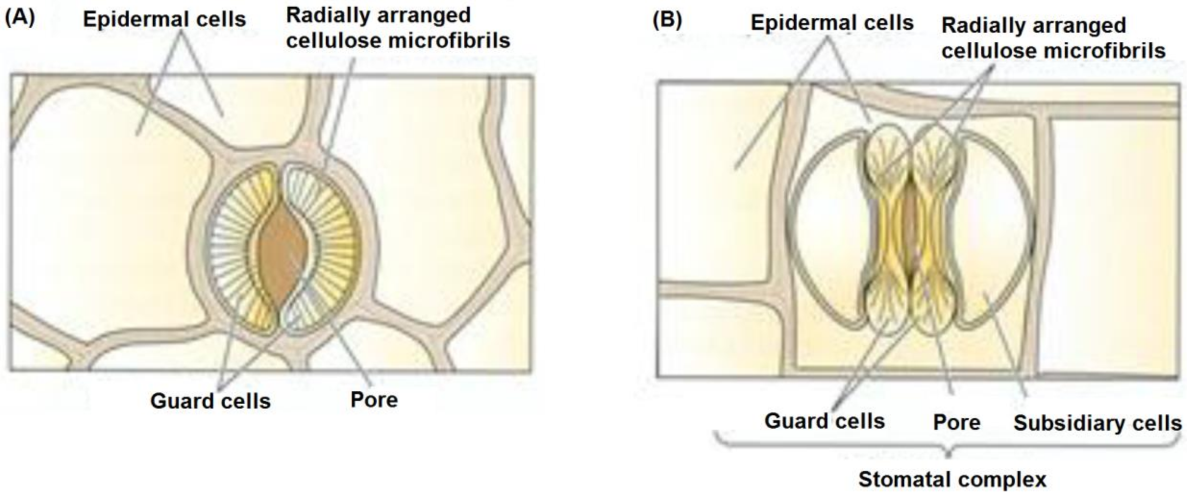


Figure 9 The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of (A) a kidney-shaped stoma and (B) a grasslike stoma.

An increase in guard cell turgor pressure opens the stomata

Guard cells function as multisensory hydraulic valves. Environmental factors such as light intensity and quality, temperature, leaf water status, and intracellular CO_2 concentrations are sensed by guard cells, and these signals are integrated into well-defined stomatal responses. The early aspects of this process are ion uptake and other metabolic changes in the guard cells. The decrease of osmotic potential (Ψs) resulting from ion uptake and from biosynthesis of organic molecules in the guard cells. Water relations in guard cells follow the same rules as in other cells. As Ψs decreases, the water potential decreases, and water consequently moves into the guard cells. As water enters the cell, turgor pressure increases. Because of the elastic properties of their walls, guard cells can reversible increase their volume by 40 to 100%, depending on the species. Such changes in cell volume lead to opening or closing of the stomatal pore. Subsidiary cells appear to play an important role in allowing stomata to open quickly and to achieve large apertures.

Chapter II Plant mineral nutrition

1. Roles of essential elements

Elements mainly derived from soil in inorganic form are known as mineral elements. The three main sources of nutrients for plants are air, water, and soil. Elements obtained from air are known as non-mineral elements, such as carbon, oxygen, and hydrogen. Irrigation water is also a source of mineral elements from dissolved salts, mainly NaCl, Na_2SO_4, $NaHCO_3$, $MgSO_4$, $CaSO_4$, $CaCl_2$, KCl, and K_2SO_4. The third environmental source of nutrition for autotrophic plants is soil.

At present, the list of essential elements includes 13 elements which are essential for all angiosperms and gymnosperms. Adding carbon, hydrogen, and oxygen makes it 16, and after the addition of nickel (a trace element), it makes a total of 17 essential elements.

Essential elements play two major roles in plants: (i) structural role and (ii) activators of enzymes. There is no sharp distinction between their roles because many elements form structural components of essential enzymes and help to catalyze the chemical reactions in which enzymes participate. Carbon, hydrogen, oxygen, nitrogen, sulfur, and magnesium perform both the functions. Magnesium is a structural constituent of chlorophyll molecules and it also activates many enzymes. A number of elements also regulate osmotic potential. Monovalent ions, potassium and chloride, control osmotic potential as well as act as activators of certain enzymes (**Table 1**).

2. Macroelements and Microelements

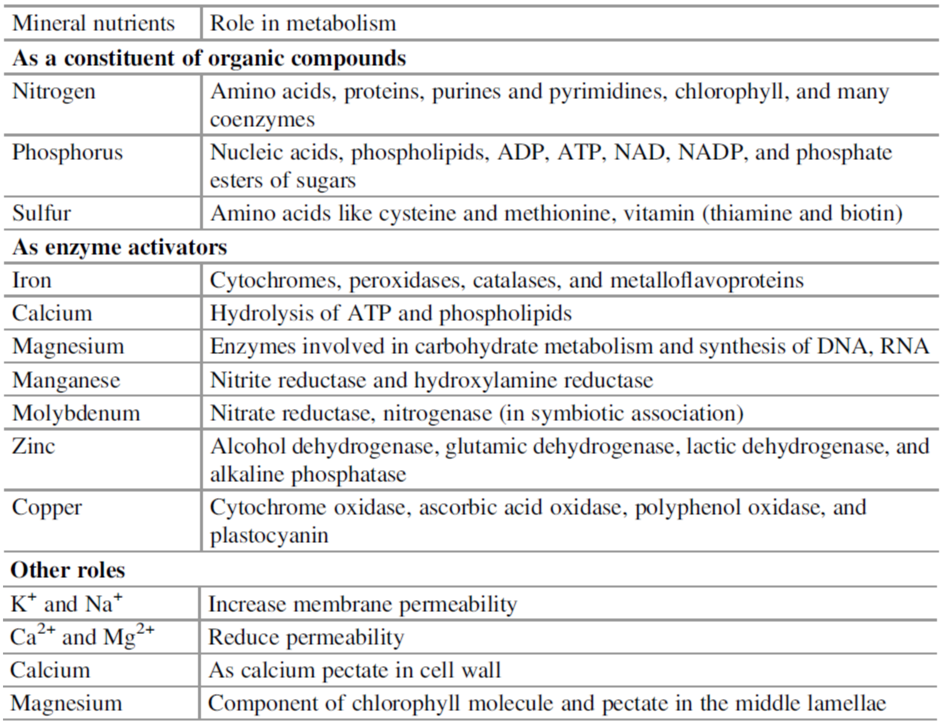
2.1. Macroelements or macronutrients

These are mineral nutrients consumed in larger quantities and are present in plant tissue in quantities ranging from 0.2% to 4.0% on dry matter weight basis. The primary macronutrients are nitrogen, phosphorus, and potassium, while secondary macronutrients include calcium, sulfur, and magnesium. Usually, potassium, calcium, and magnesium are grouped together as they are present as cations (K^+, Ca^{2+}, Mg^{2+}). Similarly, nitrogen, phosphorus, and sulfur are grouped together because they are present as anions (NO_3^-, SO_4^-, and $H_2PO_4^-$).

2.2. Microelements or Micronutrients

These are the mineral nutrients present in plant tissue in quantities measured in parts per million (ppm), ranging from 5 to 200 ppm or less than 0.02% of dry weight. Micronutrients or trace minerals are boron, chlorine, manganese, iron, zinc, copper, molybdenum, and nickel. Microelements are present as inorganic ions, oxyanions (anion with one or more oxygen atom), or undissociated molecules of boron or as organic compound complexes (chelates).

Table 1 The roles of various mineral nutrients in plant cells



Mineral nutrients	Role in metabolism
As a constituent of organic compounds	
Nitrogen	Amino acids, proteins, purines and pyrimidines, chlorophyll, and many coenzymes
Phosphorus	Nucleic acids, phospholipids, ADP, ATP, NAD, NADP, and phosphate esters of sugars
Sulfur	Amino acids like cysteine and methionine, vitamin (thiamine and biotin)
As enzyme activators	
Iron	Cytochromes, peroxidases, catalases, and metalloflavoproteins
Calcium	Hydrolysis of ATP and phospholipids
Magnesium	Enzymes involved in carbohydrate metabolism and synthesis of DNA, RNA
Manganese	Nitrite reductase and hydroxylamine reductase
Molybdenum	Nitrate reductase, nitrogenase (in symbiotic association)
Zinc	Alcohol dehydrogenase, glutamic dehydrogenase, lactic dehydrogenase, and alkaline phosphatase
Copper	Cytochrome oxidase, ascorbic acid oxidase, polyphenol oxidase, and plastocyanin
Other roles	
K^+ and Na^+	Increase membrane permeability
Ca^{2+} and Mg^{2+}	Reduce permeability
Calcium	As calcium pectate in cell wall
Magnesium	Component of chlorophyll molecule and pectate in the middle lamellae

3. Transport proteins: Ion channels and carriers

Roots transport nutrients across their plasma membrane either by diffusion down an electrochemical potential gradient or by active transport against an electrochemical potential gradient. The electrochemical potential gradient is caused by the extrusion of protons by a proton-pumping ATPase that pumps H^+ from the cytosol across the plasma membrane. This creates an electrical potential difference of approximately 80–150 mV (negative inside) across the plasma membrane (**Figure 10 A**). The proton pump functions like the ATPase in the thylakoid membrane of the chloroplast and the inner membrane of mitochondria; however, here the ATPase acts in reverse: it uses ATP and extrudes protons. Cations tend to move inward and anions outward along this electrochemical potential gradient. The Nernst equation allows us to calculate that monovalent cations are at electrochemical equilibrium (no driving force for movement) if the concentration of the cation is 40- to 150-fold less outside than inside the cell. For monovalent anions the reverse can be calculated: the concentration of an anion at electrochemical equilibrium is 40- to 150-fold less inside than outside the cell. When concentration gradients are less than this, ions may move in the direction predicted by the electrochemical gradient; when the concentration gradients exceed these values, ions may move in the opposite direction (**Figure 10 B**).

For most ions, diffusion across the lipid bilayer of the plasma membranes is a very slow process, unless facilitated by special transport proteins. Such transport proteins include ion-specific channels (i.e. ‘pores’ in the membrane through which ions can move single file). These channels function in a similar way as the water-channel (aquaporin) proteins. The ion channels are either open or closed, depending on the membrane potential or the concentration of specific molecules that affect them (**Figure 10 A**). Ion channels have the advantage that they allow massive transport, albeit only down an electrochemical potential gradient.

Although ions can move via a channel down an electrochemical potential gradient across the plasma membrane, ion transport via channels is ultimately an active process. This is because charge balance must be accomplished, by the H^+-pumping ATPase, at the expense of ATP; otherwise, membranes subjected to, say, NH_4^+ or Na^+ uniport [that is, transport that is not accompanied with the transport of H^+ in the same (co-transport) or opposite (antiport) direction] would electrically supercharge and ‘combust’ very quickly .

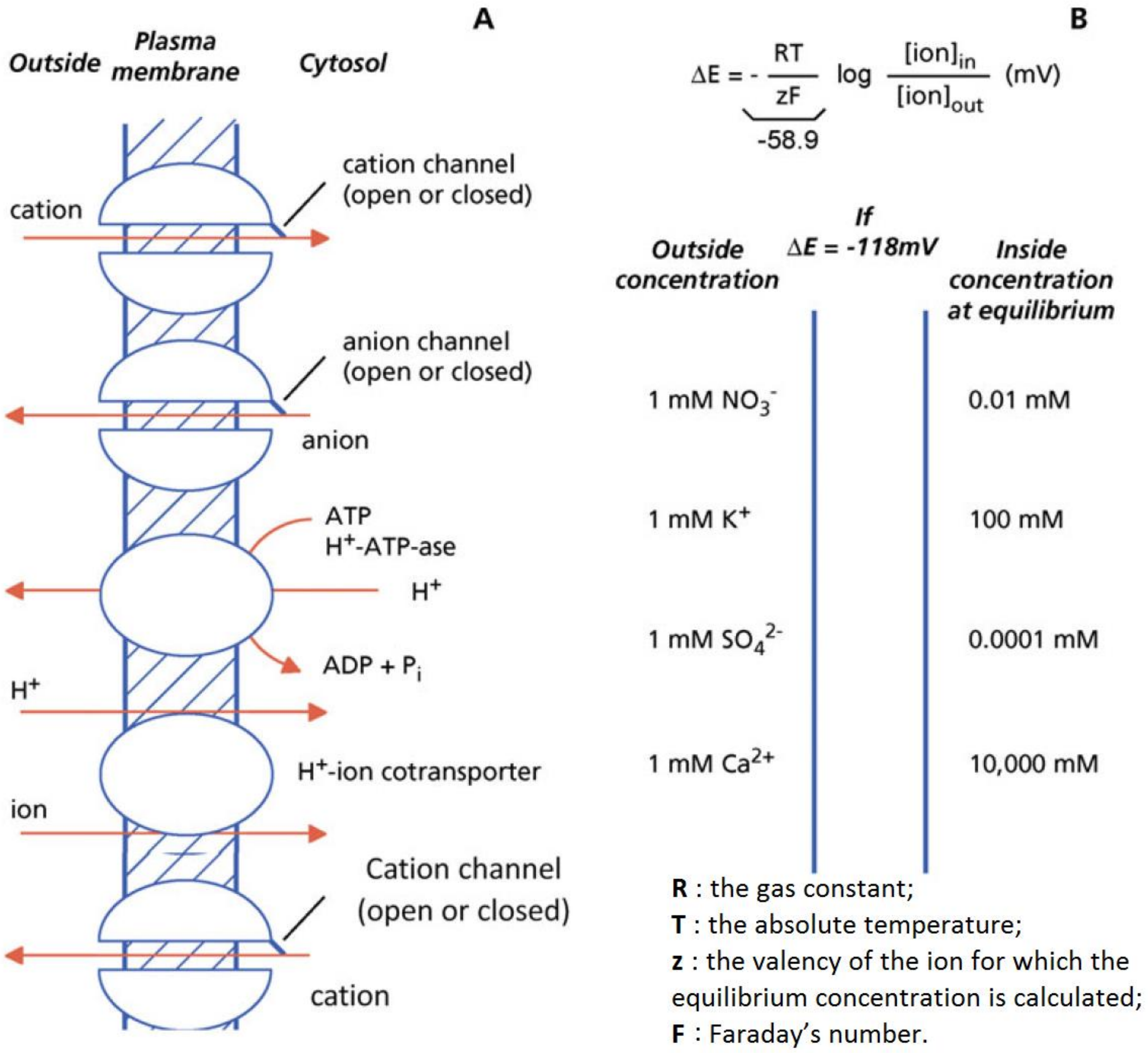


Figure 10 (A) Ion transport across the plasma membrane. The membrane potential is negative (i.e. there is a negative charge inside and a positive charge outside). (B) Schematic representation of the concentration of monovalent and divalent anions and cations that is expected if the plasma membrane is perfectly permeable for these ions in the absence of energy-requiring mechanisms at a membrane potential of 118 mV.

4. Passive and active transport

Molecular and ionic movement from one location to another is known as **transport**. Local transport of solutes into or within cells is regulated mainly by membranes. Larger-scale transport between plant organs, or between plant and environment, is also controlled by membrane transport at the cellular level. For example, the transport of sucrose from leaf to root through the phloem, referred to as **translocation**, is driven and regulated by membrane transport into the phloem cells of the leaf and from the phloem to the storage cells of the root.

According to Fick's first law, the movement of molecules by diffusion always proceeds spontaneously, down a gradient of free energy or chemical potential, until equilibrium is reached. The spontaneous "downhill" movement of molecules is termed *passive transport*. At equilibrium, no further net movements of solutes can occur without the application of a driving force. The movement of substances against a gradient of chemical potential, or "uphill", is termed *active transport*. It is not spontaneous, and it requires that work be done on the system by the application of cellular energy. One common way (but not the only way) of accomplishing this task is to couple transport to the hydrolysis of ATP (**Figure 11**).

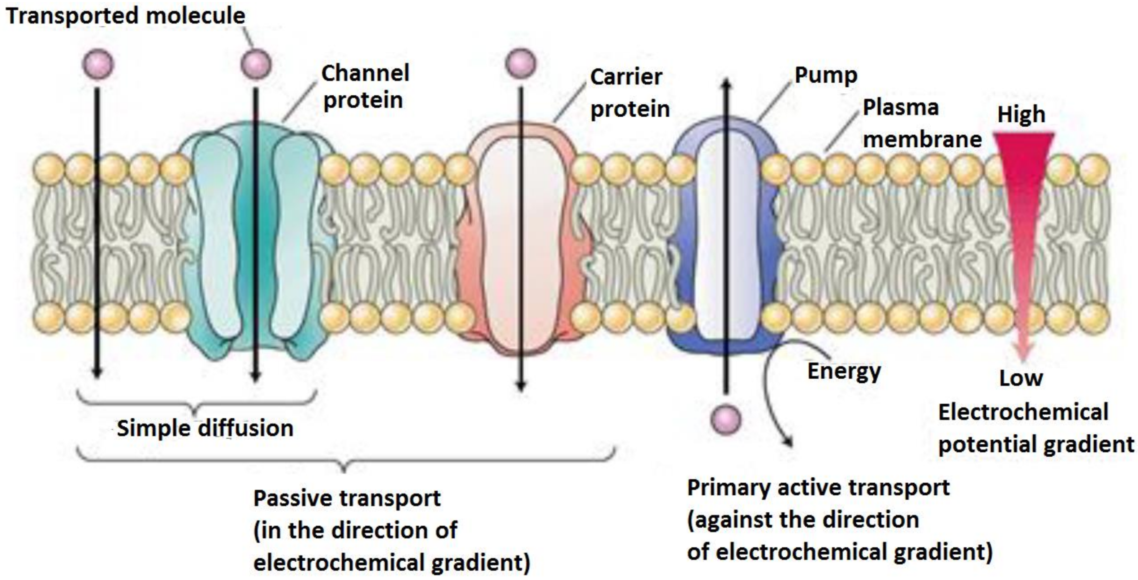


Figure 11 Three classes of membrane transport proteins: channels, carriers, and pumps

5. Solutes movement from cell to cell

In terms of the transport of small molecules, the cell wall is an open lattice of polysaccharides through which mineral nutrients diffuse readily. Because all plant cells are separated by cell walls, ions can diffuse across a tissue (or be carried passively by water flow) entirely through the cell wall space without ever entering a living cell. This continuum of cell walls is called the extracellular space, or

apoplast. Typically, 5 to 20% of the plant tissue volume is occupied by cell walls. Just as the cell walls form a continuous phase, so do the cytoplasms of neighboring cells, collectively referred to as the **symplast (see also water movement in Chapter I)**. Plant cells are interconnected by cytoplasmic bridges called *plasmodesmata*, cylindrical pores 20 to 60 nm in diameter (**Figure 12**). Each plasmodesma is lined with plasma membrane and contains a narrow tubule, the *desmotubule*, that is a continuation of the endoplasmic reticulum.

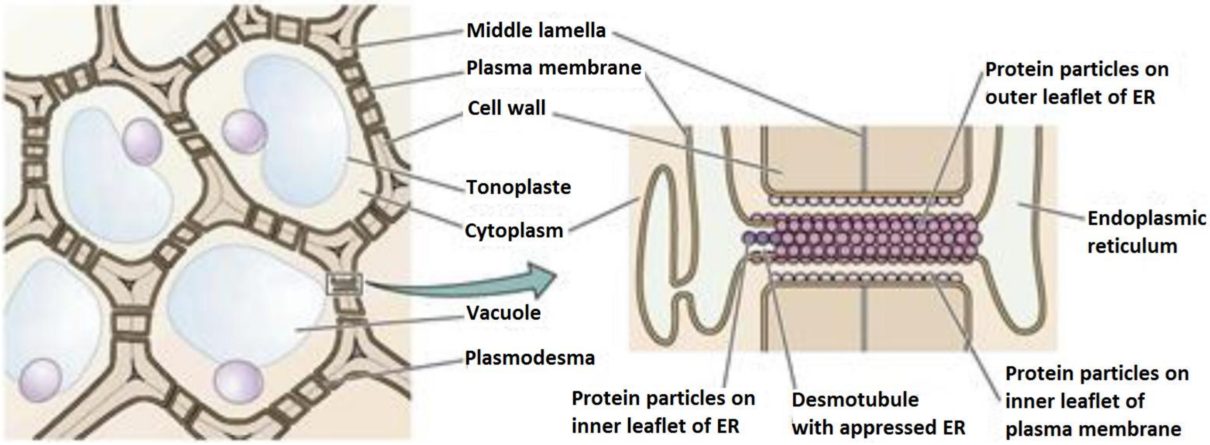


Figure 12 Plasmodesmata connect the cytoplasms of neighbouring cells facilitating cell-to-cell communication and solute transport

Chapter III. Carbon plant nutrition

1. Overview on photosynthesis

Photosynthesis is the production of reduced carbon compounds using water, carbon dioxide, light energy, and a variety of biochemical cofactors. It occurs in two main phases: the conversion of light energy to chemical energy and the fixation of carbon dioxide to carbon compounds using the fixed chemical energy taken from light. Photosynthesis takes in water and carbon dioxide, releases oxygen, and produces photosynthate. Photosynthesis takes place in a specialized organelle within the palisade parenchyma cells of the leaves called the chloroplast. Chloroplasts are tiny green discs found in virtually all plant cells that are exposed directly to the light (**Figure 13**). It is in the chloroplast that many of the nutrients required by plants are concentrated. For example, a large amount of nitrogen, iron, and magnesium in the plant is found in the chloroplast, due to their roles as structural components of the enzymes and chemicals of the photosynthetic apparatus. Nitrogen and magnesium are critical components of chlorophyll, and without sufficient quantities of these nutrients, chlorophyll cannot be formed.

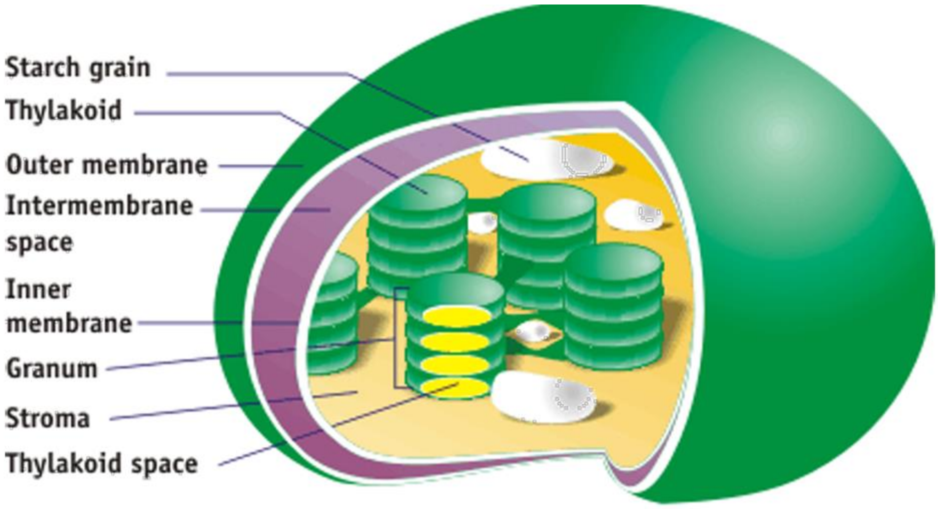


Figure 13 Structure of a Chloroplast

Failure to form chlorophyll reduces the green color of the leaves, and thus chlorosis results. Iron plays a key role in many of the compounds of the energy-harvesting complex by which the light energy is converted into chemical energy. The carbon dioxide used in photosynthesis comes from the atmosphere, and thus must flow into the interior of a leaf to be available to the chloroplasts for photosynthesis. To allow the influx through the leaves of carbon dioxide, an efflux of oxygen gas and water vapor from the leaf interior also takes place. This results in the net loss of large quantities of water. The evaporation of water from the leaf results in a bulk flow of water up from the roots to replace the lost water, and it is in this stream of water moving up the plant that most of the nutrients can be found.

The light reactions of photosynthesis involve light-driven electron and proton transfers, which occur in the thylakoid membrane, whereas the dark reactions involve the fixation of CO_2 into carbohydrate, via the Calvin–Benson cycle, which occurs in the stroma (**Figure 14**). The light reactions involve electron transfer from water to $NADP^+$ to form NADPH and these reactions are coupled to proton transfers that lead to the phosphorylation of adenosine diphosphate (ADP) into ATP. The Calvin–Benson cycle uses ATP and NADPH to convert CO_2 into carbohydrates (**Figure 14**), regenerating ADP and $NADP^+$. The light and dark reactions are therefore mutually dependent on one another.

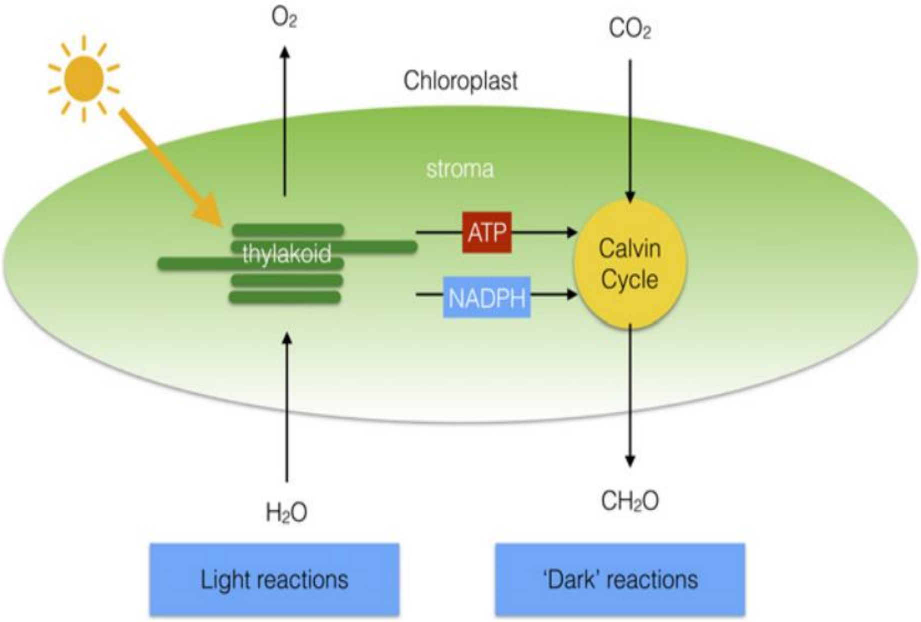


Figure 14 Division of labour within the chloroplast

The light reactions of photosynthesis take place in the thylakoid membrane, whereas the dark reactions are located in the chloroplast stroma.

2. Photosynthetic pigments

The energy of sunlight is first absorbed by the pigments of the plant (**Figure 15**). All pigments active in photosynthesis are found in the chloroplast. The **chlorophylls** and bacteriochlorophylls are the typical pigments of photosynthetic organisms. Chlorophylls *a* and *b* are found in green plants, and *c* and *d* are found in some protists and cyanobacteria. All chlorophylls have a complex ring structure that is chemically related to the porphyrin-like groups found in haemoglobin and cytochromes. The different types of **carotenoids** found in photosynthetic organisms are all linear molecules with multiple conjugated double bonds. Absorption bands in the 400 to 500 nm region give carotenoids their characteristic orange colour. Carotenoids are found in all photosynthetic organisms. The light energy absorbed by the carotenoids is transferred to chlorophyll for photosynthesis; because of this role they are called accessory pigments. Carotenoids also help to protect the organism from damage caused by light.

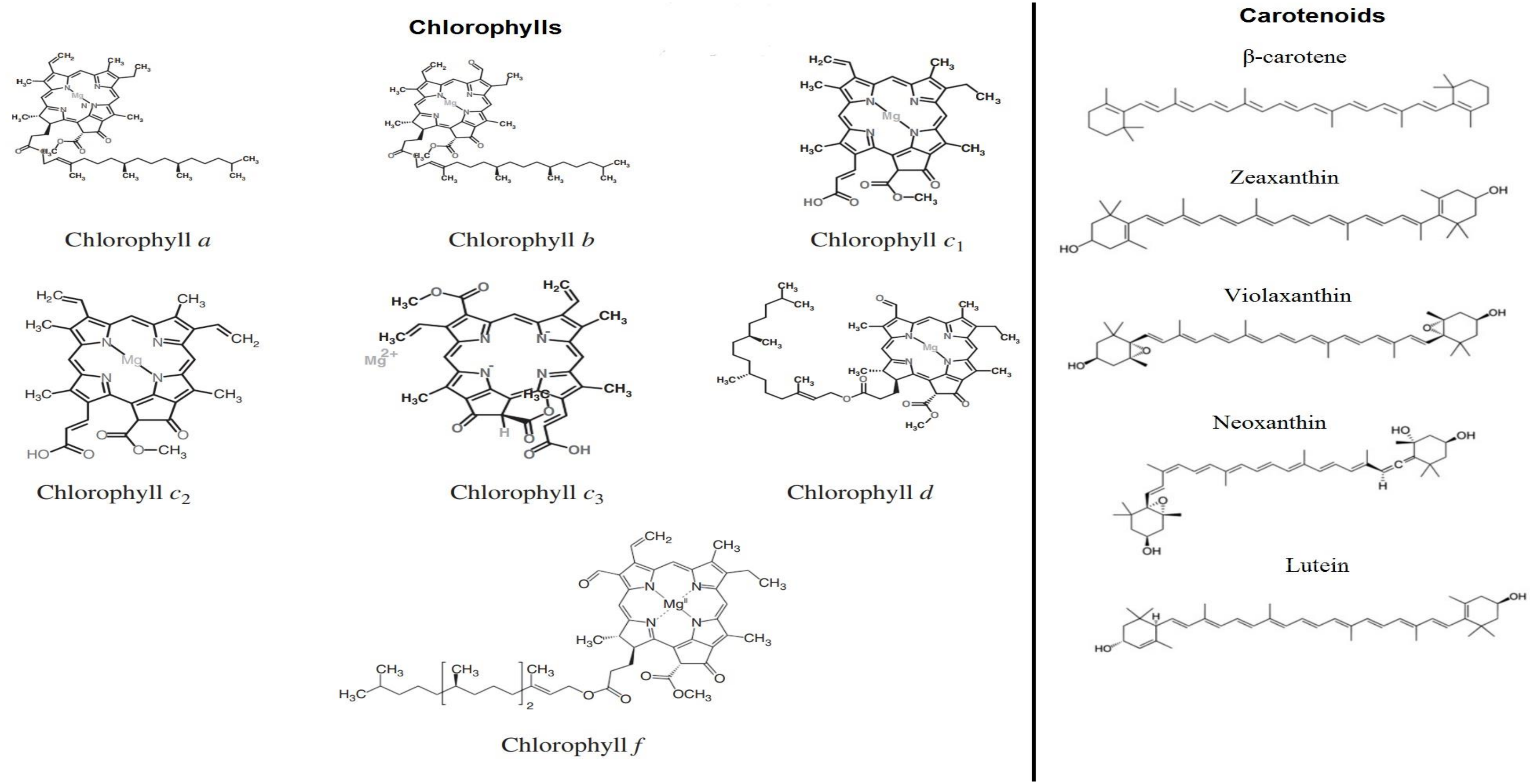


Figure 15 Major photosynthetic pigments in plants.

The chemical structures of the chlorophyll and carotenoid pigments present in the thylakoid membrane. Note the presence in each of a conjugated system of carbon–carbon double bonds that is responsible for light absorption.

3. Steps of photosynthesis mechanism

3.1. Light-harvesting antennas and photochemical reaction centers

Phycobilisomes serve as the primary light-harvesting antennae for photosystem II in cyanobacteria and red algae. These supramolecular complexes are primarily composed of phycobiliproteins, brilliantly coloured family of water soluble proteins bearing covalently attached, open-chain tetrapyrroles known as **phycobilins**. Absorbed light energy is transferred by very rapid, radiation-less downhill energy transfer from phycoerythrin or phycoerythrocyanin (if present) to C-phycocyanin and then to allophycocyanin species that act as the final energy transmitters from the phycobilisome to the photosystem II or photosystem I reaction centers.

The absorption of the light energy is a cooperation between many chlorophylls and carotenoid molecules (**Figure 16**). The majority of the pigments serve as an **antenna complex**, collecting light and transferring the energy to the **reaction center complex**, where the chemical oxidation and reduction reactions leading to long-term energy storage take place. Even in bright sunlight, a single chlorophyll molecule absorbs only a few photons each second. If there were a reaction center associated with each chlorophyll molecule, the reaction center enzymes would be idle most of the time, only occasionally being activated by photon absorption. However, if a reaction center receives energy from many pigments at once, the system is kept active a large fraction of time. Several hundred pigments are associated with each reaction center, and each reaction center must operate four times to produce one molecule of oxygen – hence the value of 2500 chlorophylls per O_2. The reaction centers and most of the antenna complexes are integral components of the photosynthetic membrane. In eukaryotic photosynthetic organisms, these membranes are found within the chloroplast; in photosynthetic prokaryotes, the site of photosynthesis is the plasma membrane or membranes derived from it.

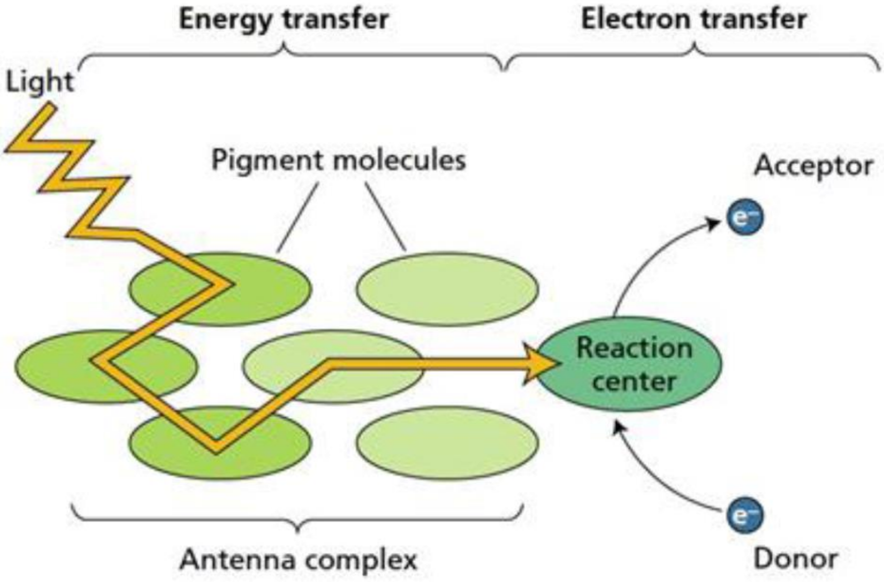


Figure 16 Basic concept of energy transfer during photosynthesis

3.2. Photosynthetic electron and proton transfer chain

The light-driven electron transfer reactions of photosynthesis begin with the splitting of water by Photosystem II (PSII). PSII is a chlorophyll–protein complex embedded in the thylakoid membrane that uses light to oxidize water to oxygen and reduce the electron acceptor plastoquinone to plastoquinol. Plastoquinol in turn carries the electrons derived from water to another thylakoid-embedded protein complex called cytochrome b6f (cytb6f). cytb6f oxidizes plastoquinol to plastoquinone and reduces a small water-soluble electron carrier protein plastocyanin, which resides in the lumen. A second light-driven reaction is then carried out by another chlorophyll protein complex called Photosystem I (PSI). PSI oxidizes plastocyanin and reduces another soluble electron carrier protein ferredoxin that resides in the stroma. Ferredoxin can then be used by the ferredoxin–NADP$^+$ reductase (FNR) enzyme to reduce NADP$^+$ to NADPH. This scheme is known as the linear electron transfer pathway or Z-scheme (**Figure 17**).

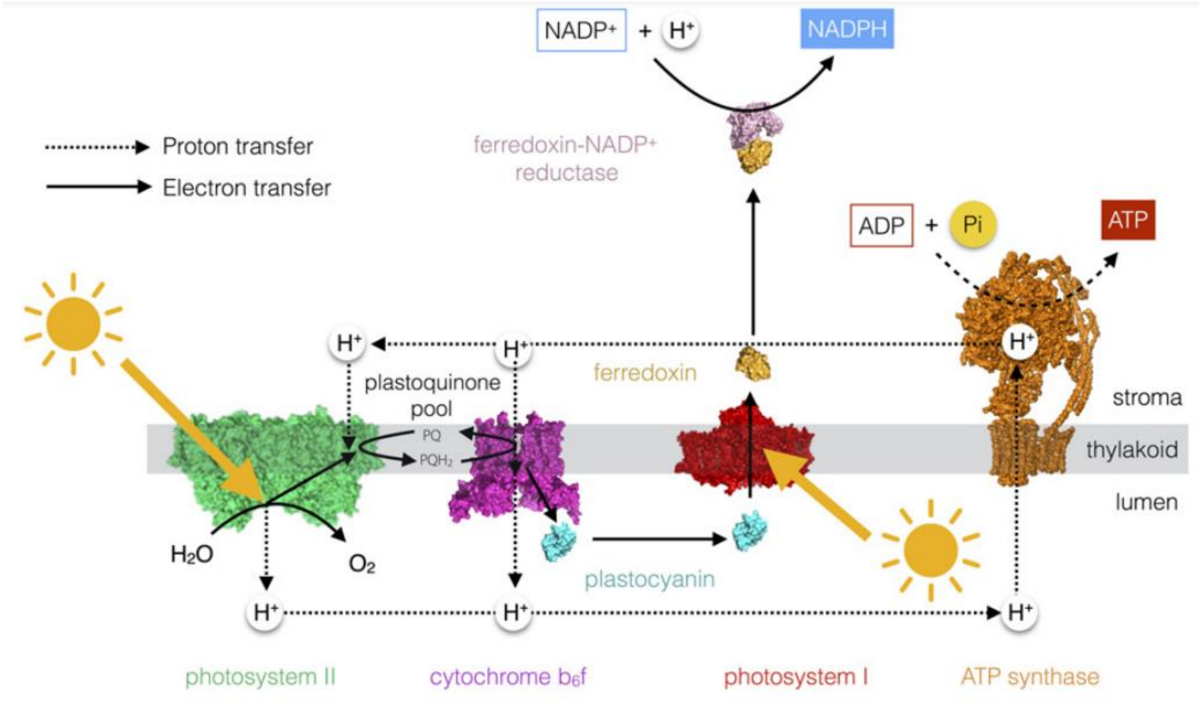


Figure 17 The photosynthetic electron and proton transfer chain

The linear electron transfer pathway, from water to NADP$^+$, to form NADPH results in the formation of a proton gradient across the thylakoid membrane that is used by the ATP synthase enzyme to make ATP.

3.3. The photosystem I reaction center reduces NADP$^+$

The PSI reaction center complex is a large multisubunit complex. In contrast to PSII, in which the antenna chlorophylls are associated with the reaction center, but present on separate pigment-proteins, a core antenna consisting of about 100 chlorophylls is an integral part of the PSI reaction center. The core antenna and P700 are bound to two proteins, PsaA and PsaB. Electrons from PSI reaction center are transferred to **ferredoxin (Fd)**, a small, water-soluble iron-sulfur protein. The membrane-associated **flavoprotein ferredoxin-NADP-reductase (FNR)** reduces $NADP^+$ to NADPH, thus completing the sequence of noncyclic electron transport that begins with the oxidation of water.

3.4. Proton transport and ATP synthesis in the chloroplast

A fraction of the captured light energy is used for light-dependent ATP-synthesis, which is known as photophosphorilation. It is widely accepted that photophosphorilation works via the **chemiosmotic mechanism**, which was first proposed in the 1960s by Peter Mitchell. Chemiosmosis appears to be a unifying aspect of membrane processes in all forms of life. The basic principle of chemiosmosis is that ion concentration differences and electric-potential differences across membranes are sources of free energy that can be utilized by the cell. Electron flow is accompanied with the proton flow from one side of the membrane to the other. The direction of proton translocation is such that the stroma becomes more alkaline (fewer H^+ ions) and the lumen becomes more acidic (more H^+ ions), as a results of electron transport. Mitchell proposed that the total energy available for ATP synthesis, which he called the **proton motive force**, is the sum of a proton chemical potential and a transmembrane electric potential. Transmembrane pH difference of one pH unit is equivalent to a membrane potential of 59 mV.

The ATP is synthesized by an enzyme complex known by several names: **ATP synthase, ATPase, and F0-F1**. This enzyme consists of two parts: a hydrophobic membrane-bound portion called F0 and a portion that sticks out into the stroma called F1 (**Figure 18**). Remarkable aspect of the ATP synthase mechanism is that the internal stalk and probably much of the F0 part of the enzyme rotate during catalysis. The enzyme is actually a tiny molecular motor. Three molecules of ATP are synthesized for each rotation of the enzyme.

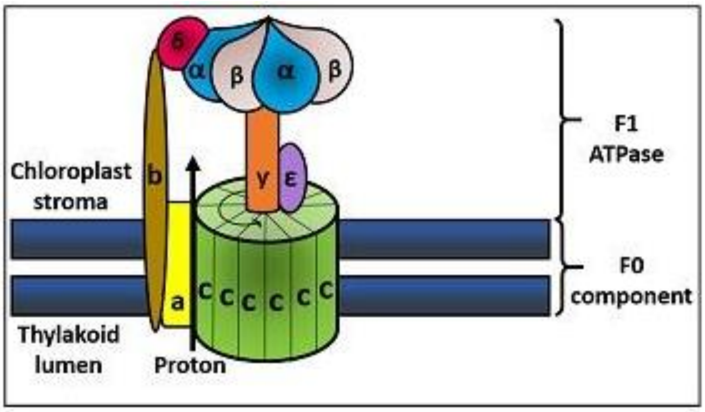


Figure 18 The structure of ATP synthase comprises two components, namely F0 and F1 ATPase.

3.5. 'Dark' reactions: the Calvin–Benson cycle

CO_2 is fixed into carbohydrate via the Calvin–Benson cycle in plants, which consumes the ATP and NADPH produced during the light reactions and thus in turn regenerates ADP, Pi and $NADP^+$. In the first step of the Calvin–Benson cycle (**Figure 19**), CO_2 is combined with a 5-carbon (5C) sugar, ribulose 1,5-bisphosphate in a reaction catalysed by the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). The reaction forms an unstable 6C intermediate that immediately splits into two molecules of 3-phosphoglycerate. 3-Phosphoglycerate is first phosphorylated by 3-phosphoglycerate kinase using ATP to form 1,3-bisphosphoglycerate. 1,3-Bisphosphoglycerate is then reduced by glyceraldehyde 3-phosphate dehydrogenase using NADPH to form glyceraldehyde 3-phosphate (GAP, a triose or 3C sugar) in reactions, which are the reverse of glycolysis. For every three CO_2 molecules initially combined with ribulose 1,5-bisphopshate, six molecules of GAP are produced by the subsequent steps. However only one of these six molecules can be considered as a product of the Calvin–Benson cycle since the remaining five are required to regenerate ribulose 1,5-bisphosphate in a complex series of reactions that also require ATP. The one molecule of GAP that is produced for each turn of the cycle can be quickly converted by a range of metabolic pathways into amino acids, lipids or sugars such as glucose. Glucose in turn may be stored as the polymer starch as large granules within chloroplasts.

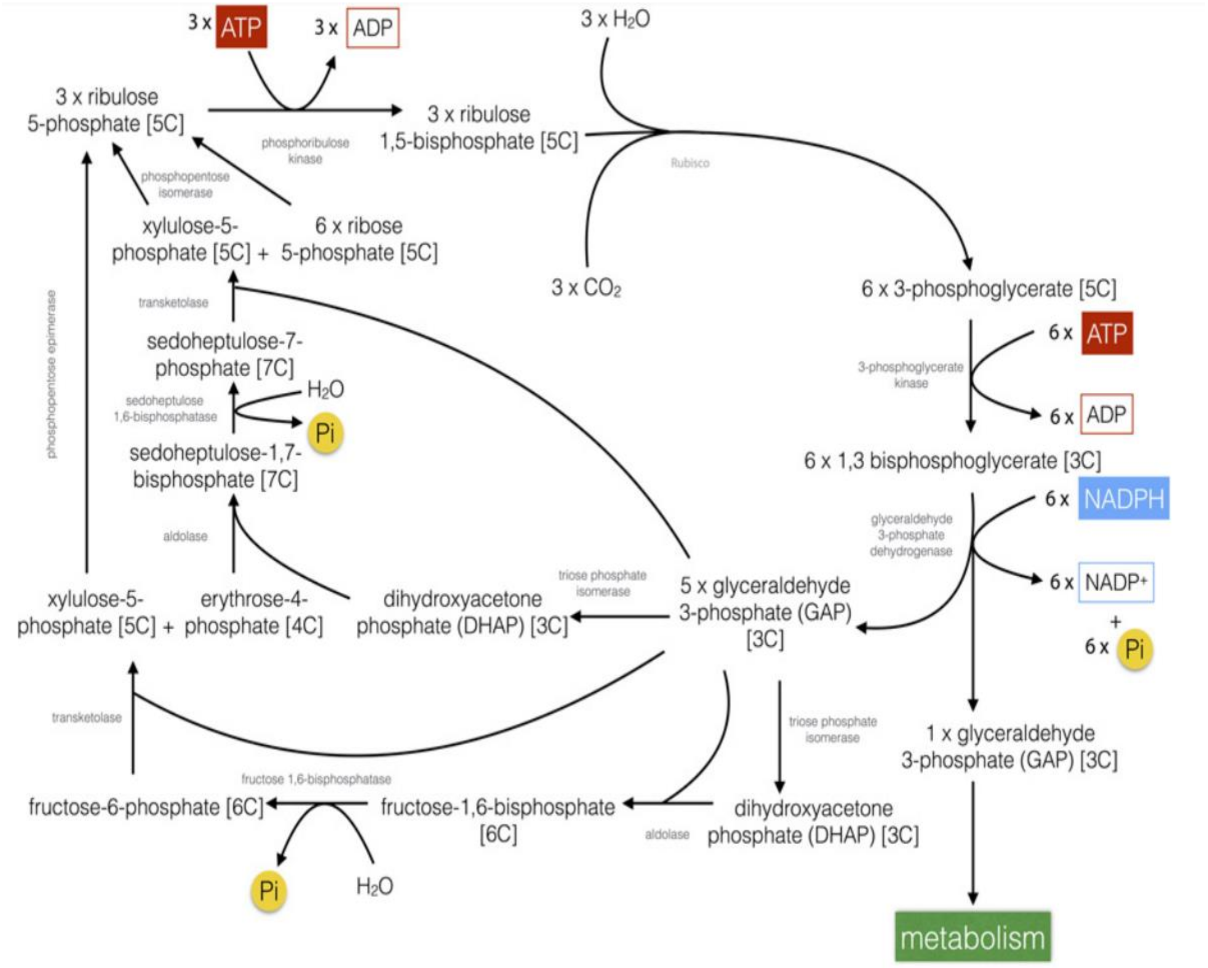


Figure 19 The Calvin–Benson cycle overview of the biochemical pathway for the fixation of CO_2 into carbohydrate in plants

Overall the synthesis of 1 mol of GAP requires 9 mol of ATP and 6 mol of NADPH, a required ratio of 1.5 ATP/NADPH. Linear electron transfer is generally thought to supply ATP/NADPH in a ratio of 1.28 (assuming an H^+ /ATP ratio of 4.67) with the shortfall of ATP believed to be provided by cyclic electron transfer reactions. Since the product of the Calvin cycle is GAP (a 3C sugar) the pathway is often referred to as C3 photosynthesis and plants that utilize it are called C3 plants and include many of the world's major crops such as rice, wheat and potato.

Many of the enzymes involved in the Calvin–Benson cycle (e.g. transketolase, glyceraldehyde-3-phosphate dehydrogenase and aldolase) are also involved in the glycolysis pathway of carbohydrate degradation and their activity must therefore be carefully regulated to avoid futile cycling when light is present, i.e. the unwanted degradation of carbohydrate. The regulation of the Calvin–Benson cycle enzymes is achieved by the activity of the light reactions, which modify the environment of the dark reactions (i.e. the stroma). Proton gradient formation across the thylakoid membrane during the light reactions increases the pH and also increases the Mg^{2+} concentration in the stroma (as Mg^{2+} flows out of the lumen as H^+ flows in to compensate for the influx of positive charges). In addition, by reducing ferredoxin and $NADP^+$, PSI changes the redox state of the stroma, which is sensed by the regulatory protein thioredoxin. Thioredoxin, pH and Mg^{2+} concentration play a key role in regulating the activity of the Calvin–Benson cycle enzymes, ensuring the activity of the light and dark reactions is closely co-ordinated.

4. Rubisco

It is noteworthy that, despite the complexity of the dark reactions outlined above, the carbon fixation step itself (i.e. the incorporation of CO_2 into carbohydrate) is carried out by a single enzyme, Rubisco. Rubisco is a large multisubunit soluble protein complex found in the chloroplast stroma. The complex consists of eight large (56 kDa) subunits, which contain both catalytic and regulatory domains, and eight small subunits (14 kDa), which enhance the catalytic function of the L subunits (**Figure 20 A**). The carboxylation reaction carried out by Rubisco is highly exergonic ($\Delta G°=-51.9\ kJ\cdot mol^{-1}$), yet kinetically very slow (just 3 s^{-1}) and begins with the protonation of ribulose 1,5-bisphosphate to form an enediolate intermediate which can be combined with CO_2 to form an unstable 6C intermediate that is quickly hydrolysed to yield two 3C 3-phosphoglycerate molecules. The active site in the Rubisco enzyme contains a key lysine residue, which reacts with another (non-substrate) molecule of CO_2 to forma carbamate anion that is then able to bind Mg^{2+}. The Mg^{2+} in the active site is essential for the catalytic function of Rubisco, playing a key role in binding ribulose 1,5-bisphosphate and activating it such that it readily reacts with CO_2. Rubisco activity is co-ordinated with that of the light reactions since carbamate formation requires both high Mg^{2+} concentration and alkaline conditions, which are provided by the light-driven changes in the stromal environment discussed above (**Figure 20 B**).

In addition to carboxylation, Rubisco also catalyses a competitive oxygenation reaction, known as photorespiration, that results in the combination of ribulose 1,5-bisphosphate with O_2 rather than CO_2. In the oxygenation reaction, one rather than two molecules of 3-phosphoglycerate and one molecule of a 2C sugar known as phosphoglycolate are produced by Rubisco. The phosphoglycolate must be converted in a series of reactions that regenerate one molecule of 3-phosphoglycerate and one molecule of CO_2. These reactions consume additional ATP and thus result in an energy loss to the plant. Although the oxygenation reaction of Rubisco is much less favourable than the carboxylation reaction, the relatively high concentration of O_2 in the leaf (250 μM) compared with CO_2 (10 μM) means that a significant amount of photorespiration is always occurring.

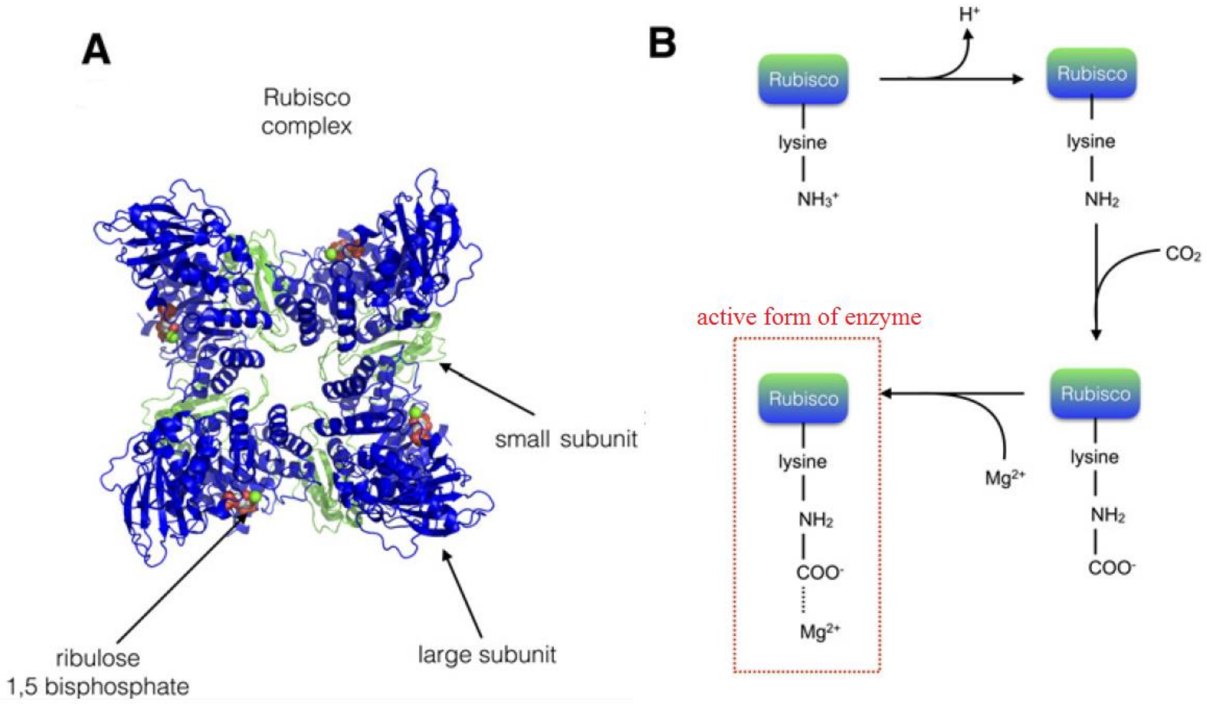


Figure 20 Rubisco enzyme

(**A**) Structure of the Rubisco enzyme (the large subunits are shown in blue and the small subunits in green); four of each type of subunit are visible in the image. Drawn from PDB code 1RXO. (**B**) Activation of the lysine residue within the active site of Rubisco occurs via elevated stromal pH and Mg^{2+} concentration as a result of the activity of the light reactions.

5. CO_2-concentrating mechanisms

To counter photorespiration, plants, algae and cyanobacteria have evolved different CO_2-concentrating mechanisms CCMs that aim to increase the concentration of CO_2 relative to O_2 in the vicinity of Rubisco. One such CCM is C4 photosynthesis that is found in plants such as maize, sugar cane and savanna grasses. C4 plants show a specialized leaf anatomy: Kranz anatomy (**Figure 21**). Kranz, German for wreath, refers to a bundle sheath of cells that surrounds the central vein within the leaf, which in turn are surrounded by the mesophyll cells. The mesophyll cells in such leaves are rich in the enzyme phosphoenolpyruvate (PEP) carboxylase, which fixes CO_2 into a 4C carboxylic acid: oxaloaceatate. The oxaloacetate formed by the mesophyll cells is reduced using NADPH to malate, another 4C acid: malate. The malate is then exported from the mesophyll cells to the bundle sheath cells, where it is decarboxylated to pyruvate thus regenerating NADPH and CO_2. The CO_2 is then utilized by Rubisco in the Calvin cycle. The pyruvate is in turn returned to the mesophyll cells where it is phosphorylated using ATP to reform PEP (**Figure 22**). The advantage of C4 photosynthesis is that CO_2 accumulates at a very high concentration in the bundle sheath cells that is then sufficient to allow Rubisco to operate efficiently.

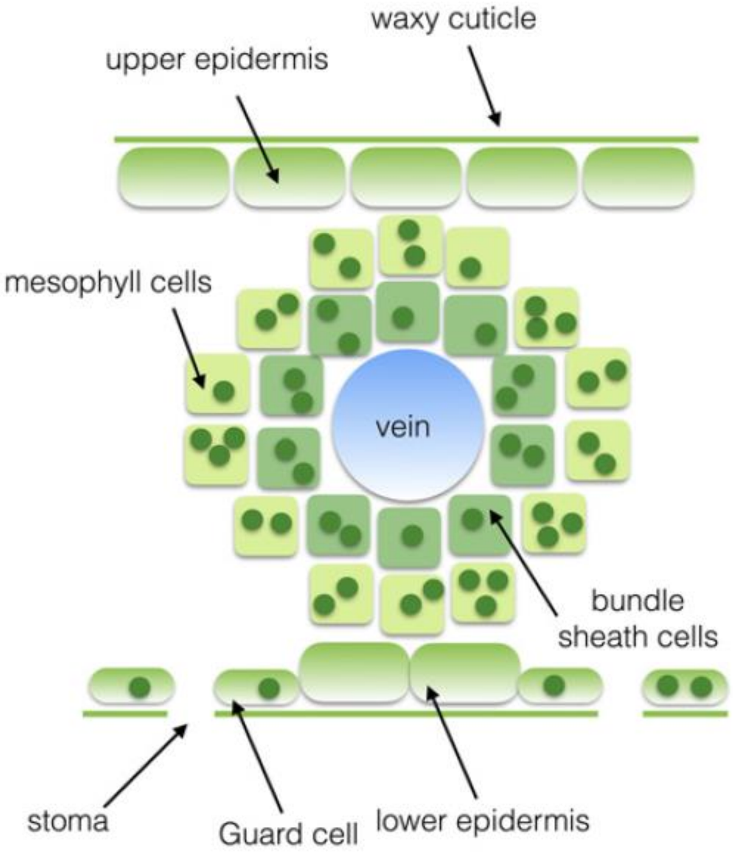


Figure 21 Diagram of a C4 plant leaf showing Kranz anatomy

Plants growing in hot, bright and dry conditions inevitably have their stomata closed for large parts of the day to avoid excessive water loss and wilting. The net result is that the internal CO_2 concentration in the leaf is very low, meaning that C3 photosynthesis is not possible. To counter this limitation, another CCM is found in succulent plants such as cacti. The Crassulaceae fix CO_2 into malate during the day via PEP carboxylase, store it within the vacuole of the plant cell at night and then release it within their tissues by day to be fixed via normal C3 photosynthesis. This is termed crassulacean acid metabolism (CAM).

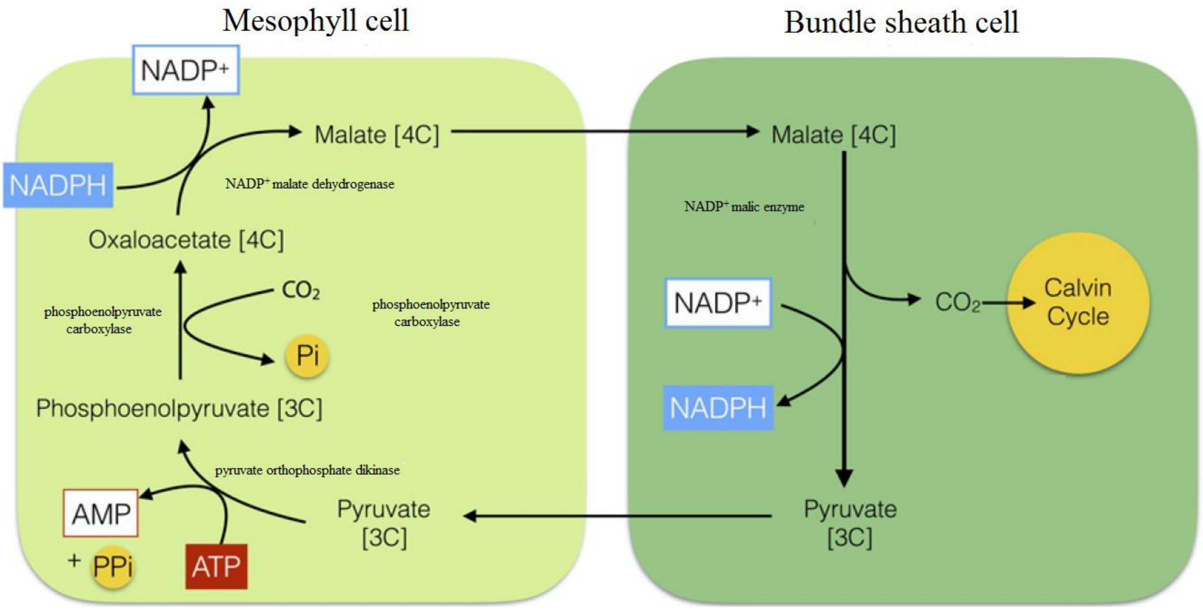


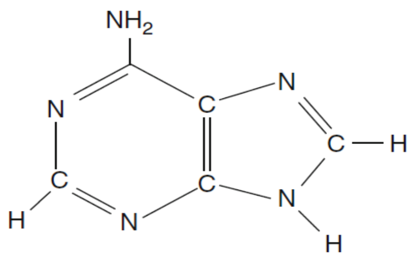
Figure 22 The C4 pathway (NADP$^+$–malic enzyme type) for fixation of CO_2

Chapter IV Nitrogen metabolism

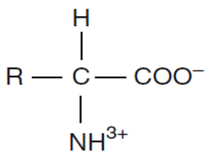
Nitrogen is one of the most important macronutrients required by the plant. All proteins consist of nitrogen-containing amino acids. Heme component of the chlorophylls, nitrogenous bases of DNA and RNA, and phenylpropanoids (such as flavonoids) are all nitrogen-containing biomolecules (**Figure 23**). Plants are not able to utilize molecular nitrogen directly. In spite of the fact that nitrogen constitutes almost 80% of the air, it needs to be provided to plants in the form of fertilizers. There are some prokaryotes, however, which have the ability to fix molecular nitrogen by means of biological fixation leading to enhancement of soil nitrogen as well. Thus, it becomes necessary to study the forms of nitrogen which plants can absorb, mechanisms of their uptake, biological nitrogen fixation, and also the mechanisms involved in their further metabolism.

1. Biogeochemical cycle of nitrogen

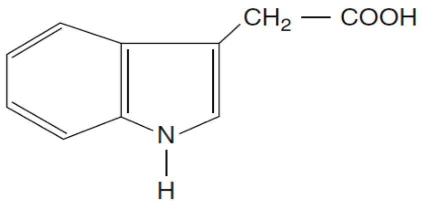
Nitrogen occurs in different forms in nature. It is present as molecular nitrogen in the air, and among living organisms, it is present in various organic forms. In soil, inorganic nitrogen is present as nitrates and ammonium ions, which are mostly derived from supplementation of fertilizers to the soil. Organic nitrogen in soil originates either from dead animals or plants or is derived from the excreta of the animals. Its source can also be the fertilizers. Some prokaryotic organisms also contribute to the nitrogen pool of the soil. These organisms are either free living or are growing in symbiotic associations with certain plants. These organic and inorganic forms of nitrogen are interconvertible which is facilitated by a number of processes responsible for the geochemical and biochemical cycle of nitrogen. The nitrogen cycle has many different steps that are as follows:



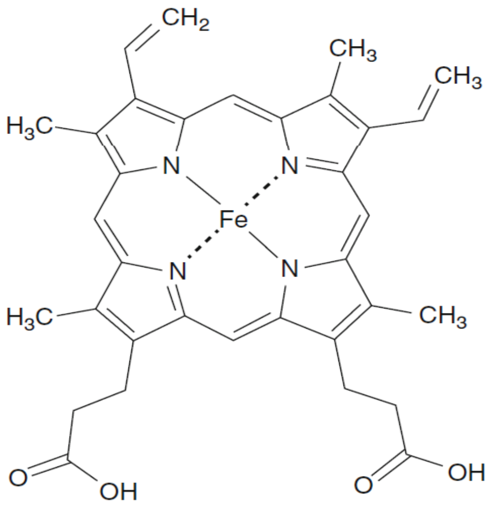
Adenine (a nitrogenous base)



α - Amino acid



Indole-3-acetic acid
(a plant hormone)



Heme (a cofactor of various hemoproteins)

Figure 23 Some of the nitrogenous biomolecules

1.1. Nitrogen fixation

Nitrogen is present in about 79% of the earth's atmosphere, but this form of nitrogen is not directly usable by most living organisms. The reduction of atmospheric nitrogen (N_2) to ammonium ions is called Nitrogen fixation. Nitrogen fixation is the process by which certain microorganisms like cyanobacteria convert atmospheric nitrogen (N_2) into ammonia (NH_3) or ammonium ions (NH_4^+). It is a very important step in the Nitrogen Cycle (**Figure 24**). Nitrogen-fixing bacteria are also present in the root nodules, Rhizobium bacteria, is an aerobic bacterium that needs some oxygen for its survival. To help them the leguminous plants have a hemoglobin-like protein called leg hemoglobin.

1.2. Ammonification

It is the process by which organic nitrogen in the soil is broken down to ammonium ions. In soil, organic nitrogen is present as amino acids, nitrogenous bases, urea, uric acid, or in various other forms of biomolecules. Dead animals, plants, and the excretory products of animals are the major sources of organic forms of nitrogen. Proteins are hydrolyzed by proteases released from microorganisms in the soil, resulting in the release of amino acids by the process known as proteolysis. At the time of ammonification, amino acids undergo oxidative deamination, and organic nitrogen is released as ammonia. The process occurs under aerobic conditions. Ammonia produced in this process gets dissolved in water resulting in the formation of ammonium ions.

$$\underset{\text{Alanine}}{C_3H_7NO_2 + \tfrac{1}{2}O_2} \longrightarrow \underset{\text{Pyruvic acid}}{C_3H_4O_3} + \underset{\text{Ammonia}}{NH_3}$$

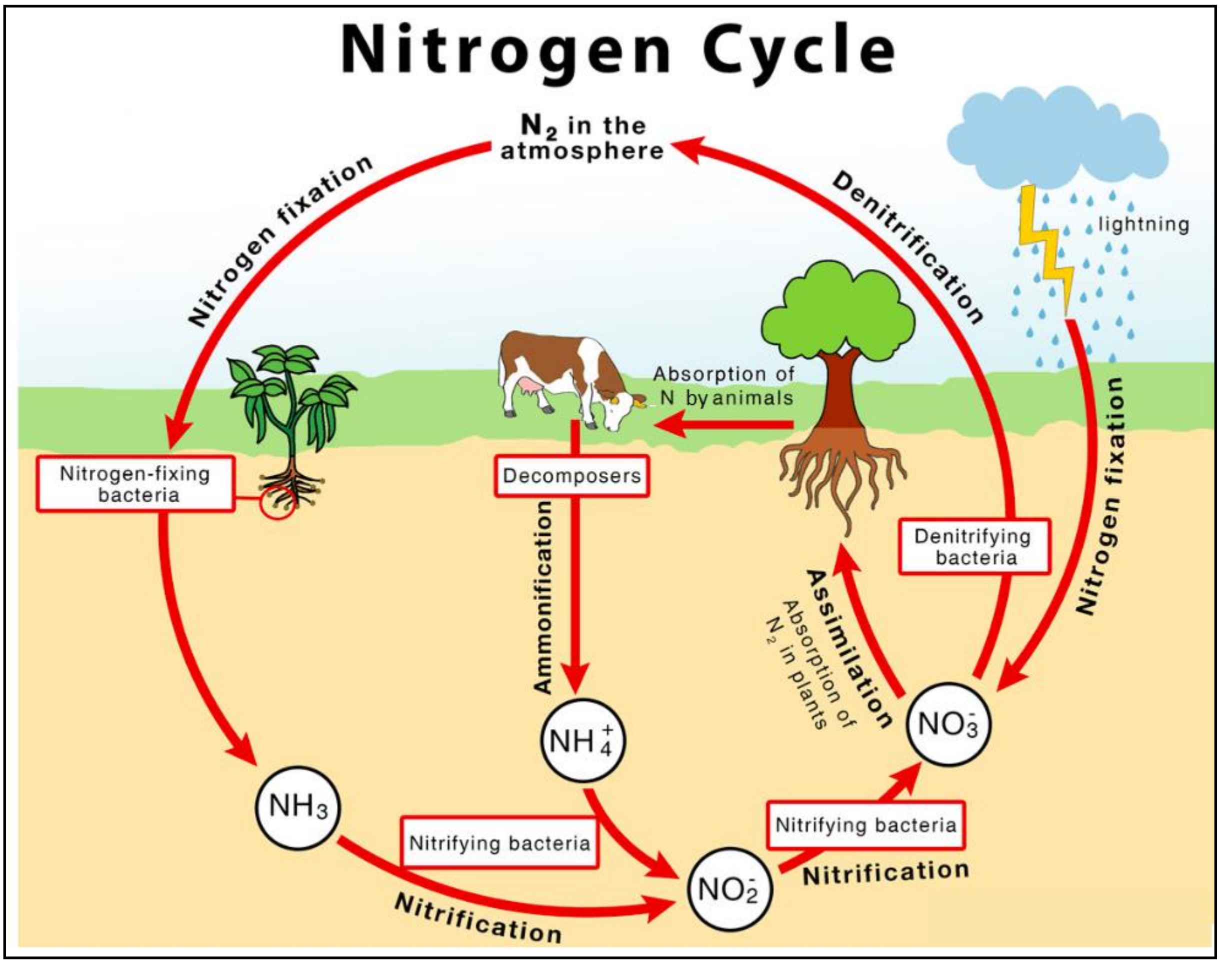


Figure 24 Different steps of nitrate conversion

1.3. Nitrification

Nitrification is a two-step process in which ammonia (NH_3) is firstly converted to Nitrates (NO_2^-) by nitrifying bacteria like Nitrosomonas and Nitrobacter. In the second step nitrate (NO_2^-) is further oxidized into Nitrate (NO_3^-) by other nitrifying bacteria like Nitrobacter. This nitrate is then taken up by the roots as it is an essential nutrient for plants. The reactions are complex and are catalyzed by various enzymes such as ammonia monooxygenase, hydroxylamine oxidoreductase, and nitrite oxidoreductase present in these bacteria.

$$NH_4^+ + 1\tfrac{1}{2}\,O_2 \rightarrow NO_2^- + H_20 + 2H^+ \qquad \left(\Delta G^{0'} = -272\ \text{kJ.mol}^{-1}\ NH_4^+\right)$$

$$NO_2^- + \tfrac{1}{2}\,O_2 \rightarrow NO_3^- \qquad \left(\Delta G^{0'} = -76\ \text{kJ.mol}^{-1}\ NO_2^-\right)$$

In some microorganisms NO_3^- serves as the electron acceptor in place of O_2 during oxidation of the substrate which gets reduced to NH_4^+ in a process known as anaerobic nitrate ammonification or nitrate respiration.

$$\boxed{C_6H_{12}O_6 + 3NO_3^- + 6H^+ \rightarrow 6CO_2 + 3NH_4^+ + 3H_2O \quad \left(\Delta G^{0'} = +1766\ \mathrm{kJ.mol^{-1}}\right)}$$

1.4. Assimilation

The nitrates and ammonia present in the soil are then taken up by the plants and primary producers and they incorporate them into their tissues to synthesize proteins, DNA, and other nitrogenous molecules. Then the consumers obtain nitrogen by consuming these plants and other animals. H^+

1.5. Denitrification

Denitrification is the final step of the nitrogen cycle, where nitrates (NO_3^-) are converted back into nitrogen gas (N_2) or nitrogen oxide (N_2O). Some of the denitrifying bacteria are *Thiobacillus denitrificans*, *Micrococcus denitrificans*, etc. This process takes place with the help of some decomposers like pseudomonas.

$$\boxed{2NO_3^- + 10e^- + 12H^+ \rightarrow N_2 + 6\ H_2O}$$

2. Nitrate uptake

Ammonium ions are short-lived in the soil as nitrifying bacteria convert them into nitrate ions. Nitrate is the most common form in which nitrogen is absorbed by plants from the soil. Generally, epidermal and cortical cells of the root absorb nitrate from the soil solution, although it can also be taken up from leaves during foliar application of fertilizers. Once inside the epidermal, cortical, or endodermal cells, further transport of nitrate into the root cells is mediated by two classes of symporters, located in plasma membrane and tonoplast, and an antiporter localized only in the tonoplast (**Figure 25**).

3. Ammonium ions

Under waterlogged conditions and in acidic soils, nitrogen is available in the form of ammonium ions because of low rates of nitrification. Unlike nitrates, ammonium ions do not easily leach out from the soil. Since they are positively charged (NH_4^+), they bind to the soil particles. Plant roots can absorb ammonium form of nitrogen into the symplasm via ammonium transporters located on the plasma membrane. High ammonium concentrations suppress the expression of the genes encoding for nitrate transporters. There are two classes of ammonium transporters (AMT) in the plants—low-affinity transporters, which are not saturated, and high-affinity saturable transporters. In the low-affinity non-saturable transporters, there is a possibility of the involvement of the aquaporins or nonselective ion channels. Proteins of low-affinity ammonium transporters, however, have not been identified so far. High-affinity transporters include transporters encoded by the AMT/Rh gene family.

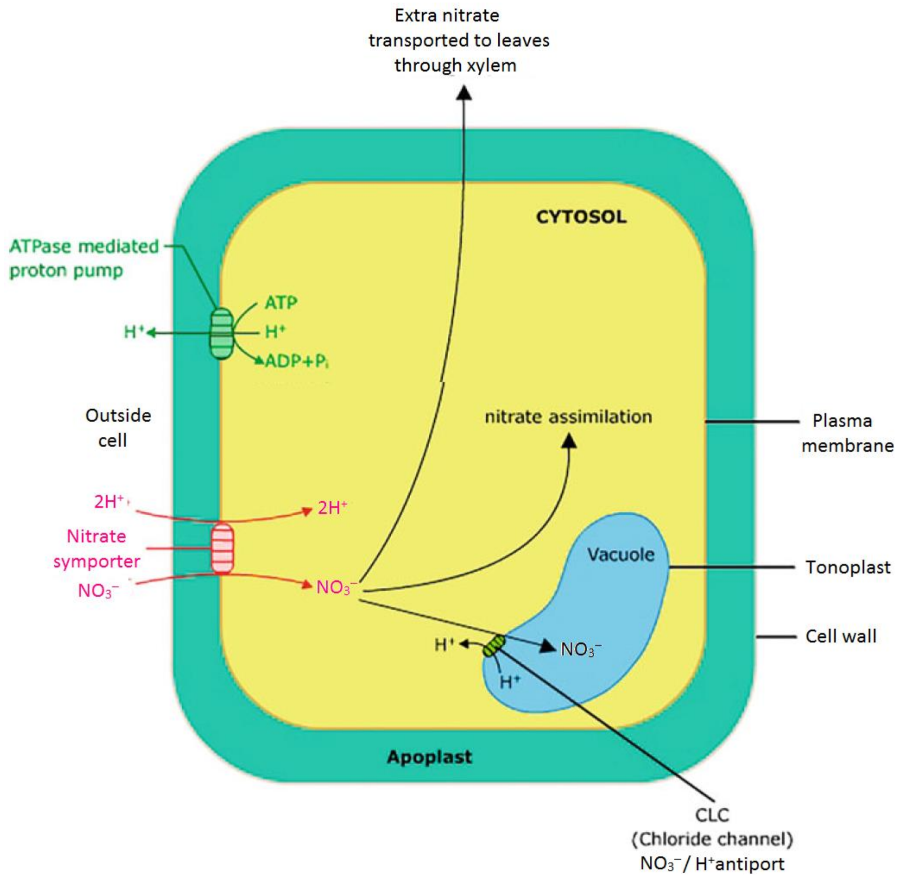


Figure 25 Nitrate uptake by a root cell

Km values of ammonium transporters range from 10 to 70 micromoles. Plant AMTs function as NH_4^+ uniporters. These transporters have multiple membrane-spanning domains. Five members of the gene family encoding AMT1 have been identified in Arabidopsis. All of them are expressed in roots, while two are expressed in shoots. NH_4^+ diffuses from soil to the symplasm of the root cells down the electrochemical gradient through the AMT1 (**Figure 26**). Once inside the cytosol, some of NH_4^+ may be converted to NH_3 due to alkaline cytosolic pH, and it may enter the vacuoles since the membranes are permeable to ammonia. Ammonia may also enter the vacuoles through aquaporins called as tonoplast intrinsic proteins (TIPs), located in the tonoplast membrane. Since NH_3 can bind with H^+ and is converted to NH_4^+ ions, it is trapped inside the vacuoles in ammonium form.

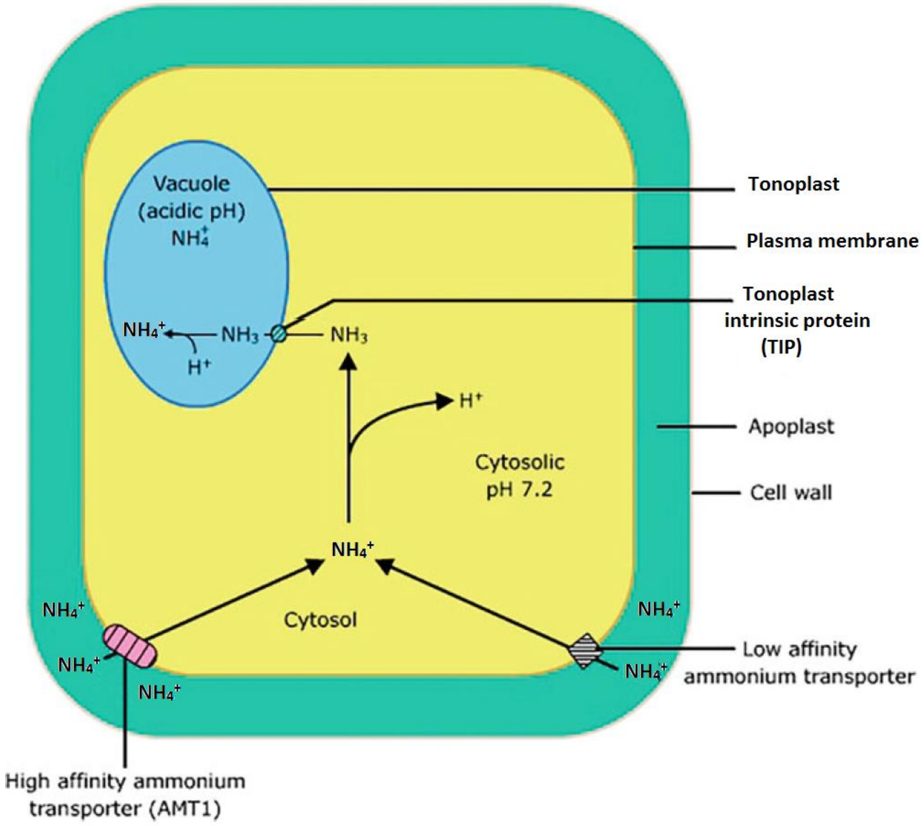


Figure 26 Ammonium ion transport in the cell

4. Nitrate Assimilation

Nitrate reduction occurs throughout in all parts of the plant except for certain species. Distribution of NR activity within plant is also governed by nitrate concentrations of available nitrate. At low concentrations (up to 1 mM), nitrate is directly assimilated in the roots of temperate legumes. If NO_3^- concentration is higher than 1 mM, its transportation to shoot becomes significant. NO_3^- transport occurs via xylem sap.

Nitrate assimilation occurs in two steps. First step requires reduction of nitrate to nitrite. It occurs in the cytosol of the cells and is catalyzed by the enzyme nitrate reductase (NR). However, nitrite reduction to ammonium occurs in plastids since the enzyme nitrite reductase (NiR) is located in the plastids.

$$\boxed{NO_3^- \xrightarrow{NR} NO_2^- \xrightarrow{NiR} NH_4^+}$$

Part 2. Growth and development

Chapter I. Seed germination

1. Structure and composition of seeds

Seeds are very diverse in their shape and size. In the mature state they contain an embryo, the next generation of plant, surrounded by a protective structure (the seed and/or fruit coat) and, in species in which the nutritive reserves are not stored within the cotyledons, by an alternative storage tissue (endosperm, perisperm, or megagametophyte) (**Figure 27**). Most seeds contain large and characteristic quantities of polymeric reserves. The major ones are carbohydrates, oils, and proteins, with minor amounts of phosphate-rich phytin. Storage in endosperm or perisperm = ***albuminous seeds***. Versus not storing in these but in cotyledons = ***exalbuminous seeds***. There are two types of seeds based on the number of cotyledons (**Figure 27**):

- **Monocotyledonous Seeds:** They contain a single cotyledon. Example: Rice
- **Dicotyledonous Seeds:** They contain two cotyledons Example: Tomato

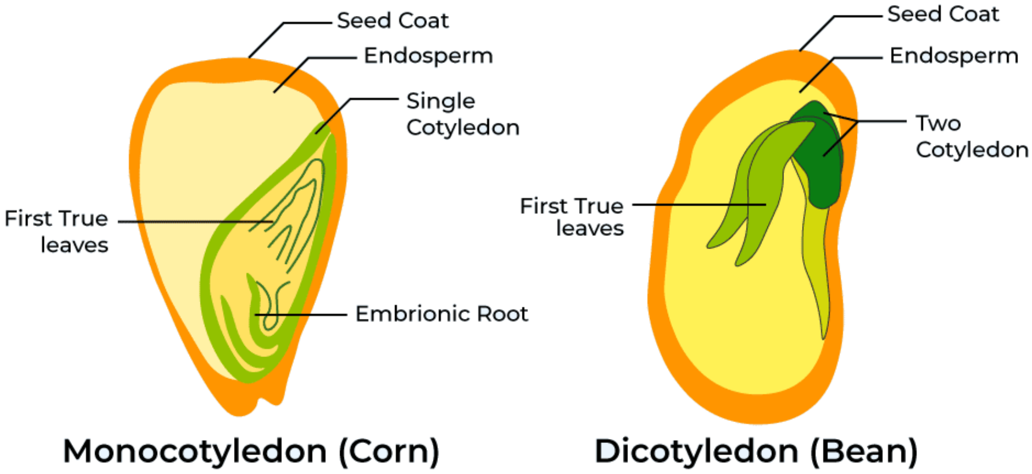


Figure 27 Seed anatomy

1.1. Seed coat

The seed coat provides protection and helps in the dispersal of seeds. The seed coat is made up of two layers: the outer testa and the inner tegmen. The **testa** is tough and protective and it prevents mechanical damage and the entry of pathogens. The **tegmen** is thin and delicate and it provides a protective covering for the embryo.

1.2. Embryo

The embryo contains the important tissues that give rise to the root, stem, and leaves of the new plant. The embryo consists of the epicotyl, the hypocotyl, the plumule, the radicle, and the cotyledons. The **plumule** is the embryonic shoot, and the **radicle** is the embryonic root.

The **epicotyl** gives rise to the shoot system above the ground, including the leaves and stem. The **hypocotyl** connects the epicotyl and the radicle. Dicot seeds have two cotyledons. In monocot seeds, only one cotyledon is present towards the lateral side of the embryonal axis which is known as ‘scutellum’ in the grass family of monocots.

1.3. Endosperm

The endosperm serves as a nutrient reservoir and provides nourishment to the developing embryo. It is rich in carbohydrates, proteins, and lipids. It is triploid(3n). Monocot seeds retain the endosperm even after germination. Also, the aleurone layer, made up of protein, covers the endosperm in monocots. The endosperm is primarily starch in the case of rice. This aleurone layer contains an enzyme known as Amylase that digests starch.

While in most dicot seeds endosperm is consumed completely during germination. The cotyledons are responsible for storing nutrients and providing nourishment to the developing embryo.

1.4. Perisperm

The persistent nucellus is known as the perisperm. It is not present in all seeds. Nucellus normally gets used up in the development of the embryo sac. If remained, then known as perisperm. Perisperm is present in seeds of sugar beet, black pepper, etc.

2. Seed development

The development of a seed begins with the fertilized ovule, or zygote. The early stage of seed development is characterized by extensive cell divisions that form the embryo and, in endospermic seeds, the tissues that store nutrients will support the eventual germination of the seed and seedling development.

The first division of the zygote is usually transverse and immediately establishes polarity of the embryo. The upper cell is destined to become the embryo itself while the lower cell produces a stalk-like suspensor that anchors the embryo at the base of the embryo sac. The typical dicot seed will then pass through several recognizable stages (**Figure 28**). During the early stages of embryo development, cell division occurs throughout the entire cell mass but at the heart-shape stage both the shoot and root apical meristems begin to organize as centers of cell division.

3. What is seed germination?

In the scientific literature the term *germination* is often used loosely and sometimes incorrectly, and so it is important to clarify its meaning. *Germination begins with water uptake by the seed (imbibition) and ends with the emergence of the embryonic axis, usually the radicle, through the structures surrounding it.* This latter event is sometimes referred to as “visible germination,” at which point the seed has completed germination (or germinated). Germination *sensu stricto* does not include seedling growth; this commences after germination is completed (**Figure 29**). A seed that is mature and dry is said to be *quiescent*. Quiescent seeds are resting organs, generally having low moisture contents (5–15%) with metabolic activity almost at a standstill. When dry, viable seeds imbibe water, a chain of events is initiated which ultimately results in the emergence of the embryo, usually the radicle, signifying that germination has been successfully completed.

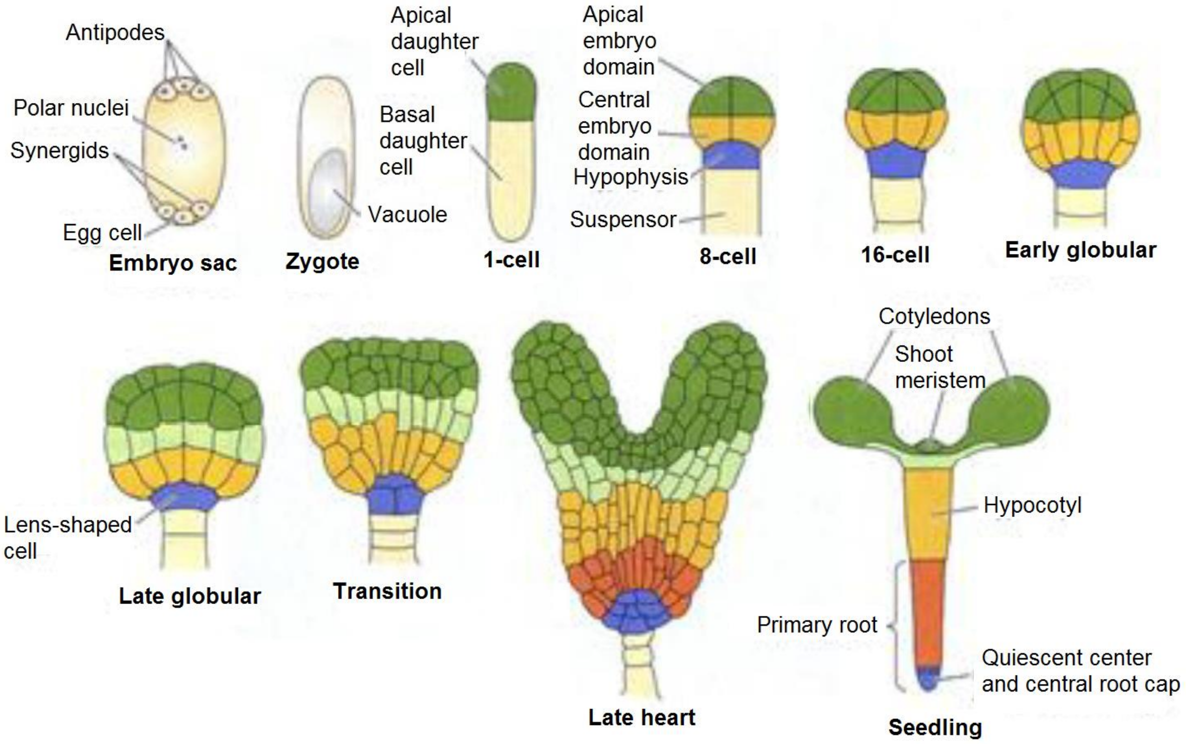


Figure 28 Pattern formation during Arabidopsis embryogenesis

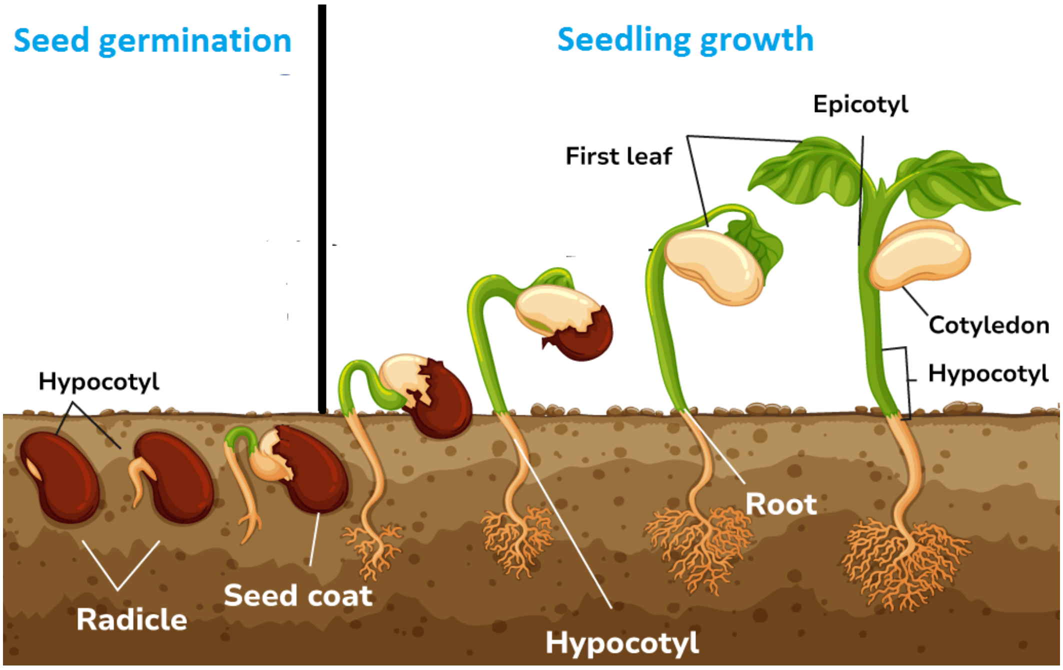


Figure 29 Diagram of Seed Germination and initial seedling growth

4. Steps of germination

Beginning in most cases from an air-dry state, seeds must first imbibe water in order to activate metabolic processes. The initial uptake of water is a physical process driven by the matric potential of the seed constituents and occurs in both living and dead seeds. In most cases, viable seeds show a three-phase pattern of water uptake, where the initial rapid uptake is followed by a plateau phase of variable duration that ends with the resumption of water uptake associated with embryo growth (**Figure 30**).

4.1. Phase I: *Seed imbibition*

As seed water content increases during this phase of imbibition (**Figure 30**), initially strong binding sites, then weak binding sites, and finally multimolecular binding sites for water become saturated. Rates of water uptake into dry seeds are controlled initially by the permeability of the testa, which may contain lignified cells and a waxy covering limiting water penetration. Water enters most rapidly through the most permeable regions of the testa, which in cereals and many other seeds is in the micropylar region, and then spreads throughout the seed tissues.

4.2. Phase II: *The lag phase*

Following the initial rapid water uptake during Phase I, water uptake rate slows and seed water content either is constant or slowly increases during Phase II of imbibition (**Figure 30**). There are two ways that further water uptake and swelling are prevented during Phase II. The embryo cells can develop turgor, an internal hydraulic pressure that offsets the osmotic gradient for water uptake. Alternatively, the tissues external to the embryo can restrict the expansion of the embryo. That is, as the embryo expands due to water uptake, it presses against the more rigid enclosing tissues (either endosperm or testa), which then limit further expansion.

4.3. Phase III: *Completion of germination*

Although dormant seeds may achieve Phase II, only seeds that complete germination enter Phase III of imbibition, which occurs due to the cellular expansion associated with radicle protrusion. Thus, water uptake during Phase III is not properly imbibitions per se, but rather the initial consequence of the completion of germination. As plant cells expand by absorbing water and stretching their cell walls, the increase in water uptake during Phase III indicates the initiation of embryo growth into a seedling as germination is completed. Endosperms and nonpersistent (hypogeal) cotyledons do not expand and hence do not show a Phase III of water uptake: eventually their water contents decline as degeneration (programmed cell death) occurs.

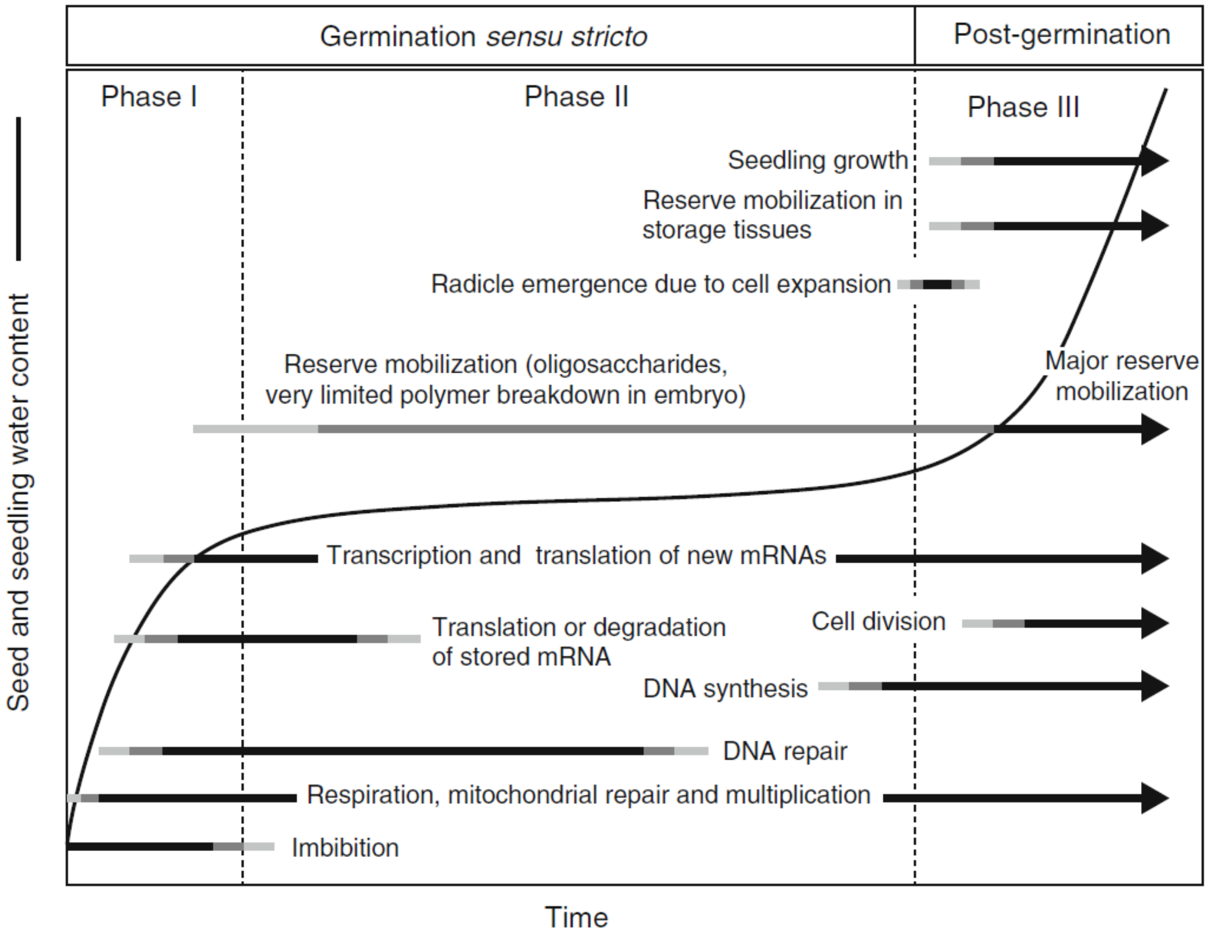


Figure 30 Time course of water uptake and some important changes associated with germination and early seedling growth.

5. Types of germination

There are two different types of germination (**Figure 31**):

5.1. Epigeal

Epigeal germination involves fastest growth of the hypocotyl, the part of the stem between the cotyledon stalks and the radicle, with the cotyledons appearing above the soil surface. Sunflowers, Acers, sycamore and French beans all show epigeal germination.

5.2. Hypogeal

Hypogeal germination involves rapid elongation of the epicotyl, the region of stem just below the pumule, with the cotyledons remaining below the surface (Hypo = below). Broad bean, horse chestnut and oak all show hypogeal germination.

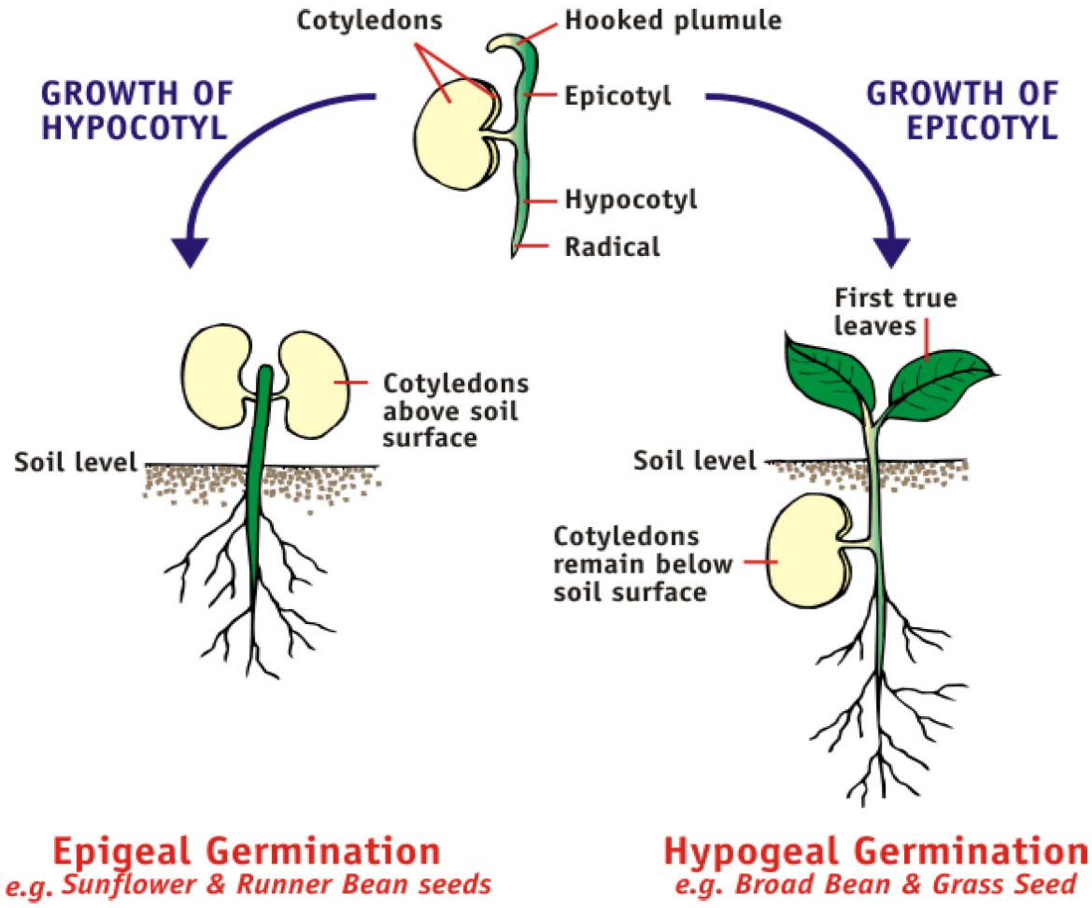


Figure 31 Types of germination

6. Factors affecting seed germination

The conditions necessary for seed germination typically include:

- **Water**: Water is very important for seed germination as it serves several essential functions. Firstly, it hydrates the protoplasm enabling vital cellular activities. Additionally, water provides dissolved oxygen necessary for the embryos growth. It also softens the seed coats enhancing seed permeability.
- **Oxygen**: Oxygen is an energy source necessary for seed growth. During germination, it fuels metabolic processes and utilised in aerobic respiration until the seed can develop its own green leaves.
- **Temperature**: Seeds require a moderate temperature range of approximately 25-30°C for germination. However, optimal temperatures vary among different seed types.
- **Light or darkness**: Sunlight serves as an environmental trigger for many seeds, prompting their germination only when exposed to its rays.
- **Soil depth**: Seed are planted at the appropriate depth ensuring they receive the right amount of warmth, moisture and oxygen for the germination of seed.

Chapter II. Plant growth

1. What is growth?

Growth is the increment in dry mass, volume, length, or area that results from the division, expansion, and differentiation of cells. Increment in dry mass may not coincide with changes in each of these components of growth. For example, leaves often expand and roots elongate at night, when the entire plant is decreasing in dry mass, because of carbon use in respiration. On the other hand, a tuber may gain dry mass without concomitant change in volume, as starch accumulates. Discussion of ‘growth’, therefore, requires careful attention to context and the role of different processes at different times. For example, cell divisions often initiate growth, but cell division by itself is insufficient to cause growth. In addition, growth requires cell elongation and the deposition of mass in the cytoplasm and cell walls, which determines the increment in volume or mass. To appreciate ecophysiological aspects of plant growth, we must understand its cellular basis. Although this is a fascinating and rapidly moving field, many questions remain unanswered, as we will reveal in this chapter.

2. Growth of whole plants and individual organs

Plant growth could be analyzed in terms of an increase in total plant dry mass and its distribution (allocation) among organs involved in acquisition of aboveground or belowground resources. In such an approach, the pattern of biomass allocation plays a pivotal role in determining a plant’s access to resource, and therefore its growth rate. We can also study plant growth at the level of individual organs or cells. Using this approach, we can ask why the leaves of one plant grow faster or bigger than those of another. The two approaches are complementary, and we should integrate them to highlight traits that determine a plant’s growth potential.

Growth analysis provides considerable insight into the functioning of a plant as dependent on genotype or environment. Different growth analyses can be carried out, depending on what is considered a key factor for growth. Leaf area and net assimilation rate are often considered ‘driving variables’; however, the plant’s nutrient concentration and nutrient productivity could also be considered as driving variables. In either case, ‘driving variables’ represent aspects of a plant’s suite of traits, rather than offering a mechanistic explanation for differences in growth rate.

3. Plant differentiation

In the phase of embryogenesis, the single-celled zygote elaborates a rudimentary but polar organization that features groups of undetermined cells contained in the shoot and root apical **meristems**. During vegetative growth, indeterminate patterns of growth, which reflect inputs from both intrinsic programs and environmental factors, yield a variable shoot and root architecture. Further, in reproductive development, vegetative shoot apical meristems are reprogrammed to produce a characteristic series of floral organs, including carpels and stamens, in which the haploid gametophytic generation begins.

3.1. The nature of plant meristems

Unlike animals, which are characterized by a generalized growth pattern, plant growth is limited to discrete regions where the cells retain the capacity for continued cell division. These regions are called **meristems**. Two such regions are the *apical meristems* located at the tips of roots and stems. These regions of active cell division are responsible for *primary growth*, or the increase in the length of roots and stems.

3.2. Meristems are centers of plant growth

The ***shoot apical meristem (SAM)*** is structurally more complex than the root apical meristem (**Figure 32**). This is understandable because in addition to producing new cells that elongate and extend the length of the axis of the shoot, the shoot apical meristern must also form primordia that give rise to lateral organs such as leaves, branches, and floral parts. Similar to the root apical meristem, each time a cell divides in the SAM, one daughter cell is left behind to elongate and move the shoot apex forward while the other daughter cell remains within the meristem to continue dividing.

The tip of the root is covered by a root cap, which provides mechanical protection for the meristem as the root grows through the abrasive soil medium. The root cap also secretes polysaccharides, which form a mucilaginous matrix called mucigel. Mucigel lubricates the root tip as it moves through the soil. The root cap along with its coating of mucigel is also involved in perception of gravity by roots. The ***root apical meristem (RAM)*** is a cluster of dividing cells located at the tip of the root just behind the root cap (**Figure 32**). Each time a cell in the meristem divides, one of the two daughter cells will be retained to continue cell division while the second daughter cell proceeds to elongate, thus increasing the length of the root and pushing the root tip through the soil. In the center of the meristem is a region of slowly dividing cells called the *quiescent zone*. Cell divisions responsible for new tissues in the elongation root and regeneration of the root cap take place around the periphery of the quiescent zone.

3.3. Tunica-corpus theory

In contrast to apical cell theory and histogen theory tunica-corpus theory is applicable only to shoot apex and not to root. Schmidt distinguishes two tissue zones in the shoot apex and termed them as tunica and corpus (**Figure 33**). Tunica is the peripheral tissue zone of shoot apex. It consists of one or more peripheral layers of cells. Dicotyledons exhibit one to five layers of cells in tunica; two layers of cells are represented by largest number of species. This region division reflects to the surface growth in the apex. As a result tunica grows as a sheet but not in thickness. Corpus is the inner tissue zone of shoot apex. It consists of cells that are several cell layers deep. Tunica overarches corpus. Meristematic tissues composing this zone are larger than tunica. The initial cells divide periclinally and the derivatives divide to form the core of the shoot apex. As a result the shoot apex increases in volume. Generally corpus is destined to give rise cortex and vascular tissue.

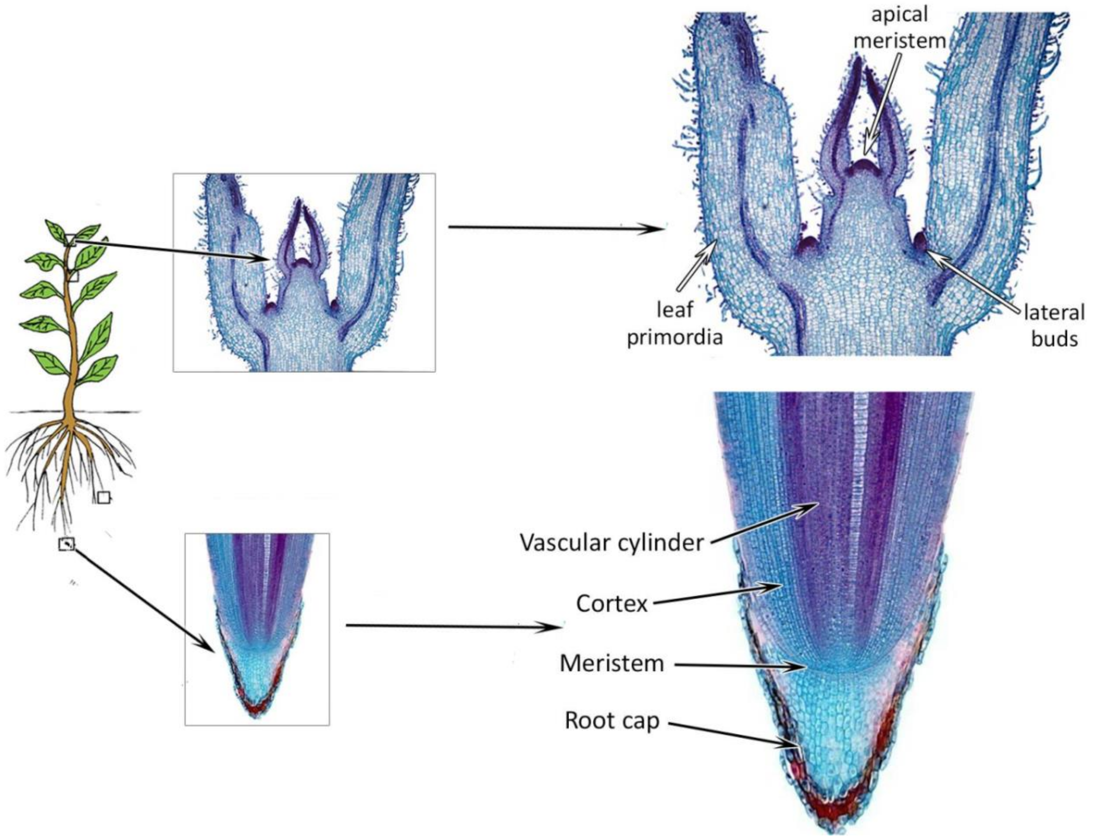


Figure 32 The main growing points in plants are the shoot and root meristems

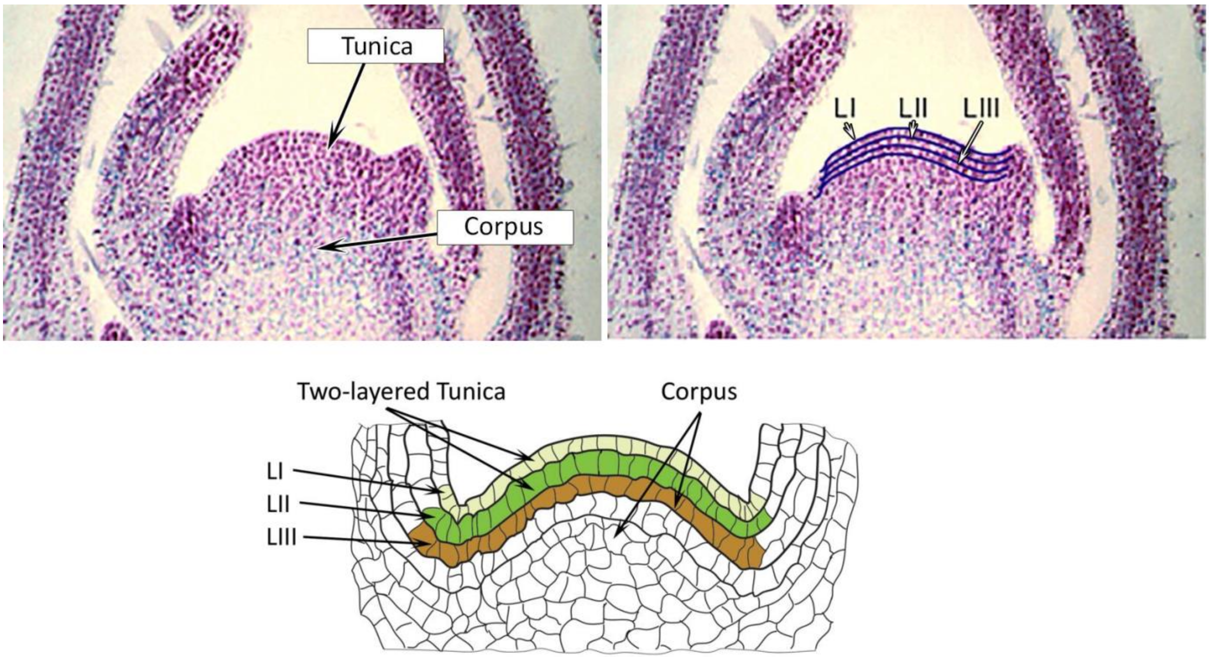


Figure 33 Tunica of the dicot shoot meristem as having distinct layers. tunica layers are called L-I, L-II, and L-III.

4. Phases of growth

The period of growth is generally divided into three phases, namely, meristematic, elongation and maturation (**Figure 34**). Let us understand this by looking at the root tips. The constantly dividing cells, both at the root apex and the shoot apex, represent the meristematic phase of growth. The cells in this region are rich in protoplasm, possess large conspicuous nuclei. Their cell walls are primary in nature, thin and cellulosic with abundant plasmodesmatal connections. The cells proximal (just next, away from the tip) to the meristematic zone represent the phase of elongation. Increased vacuolation, cell enlargement and new cell wall deposition are the characteristics of the cells in this phase. Further away from the apex, i.e., more proximal to the phase of elongation, lies the portion of axis which is undergoing the phase of maturation. The cells of this zone, attain their maximal size in terms of wall thickening and protoplasmic modifications. Most of the tissues and cell types you have studied in earlier classes represent this phase.

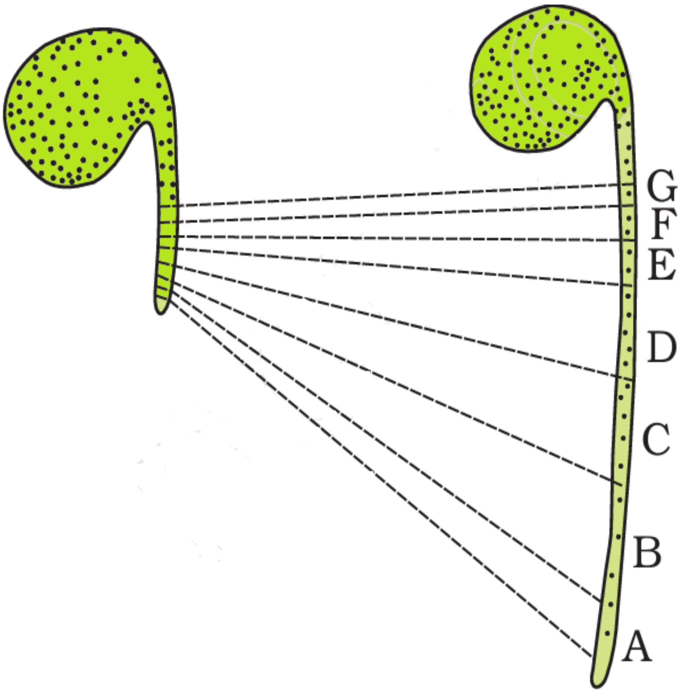


Figure 34 Detection of zones of elongation by the parallel line technique. Zones A, B, C, D immediately behind the apex have elongated most.

5. Growth rates

The increased growth per unit time is termed as growth rate. Thus, rate of growth can be expressed mathematically. An organism, or a part of the organism can produce more cells in a variety of ways. The growth rate shows an increase that may be arithmetic or geometrical (**Figure 35**).

5.1. Arithmetic growth

In arithmetic growth, following mitotic cell division, only one daughter cell continues to divide while the other differentiates and matures. The simplest expression of arithmetic growth is exemplified by a root elongating at a constant rate.

5.2. Geometrical growth

In most systems, the initial growth is slow (lag phase), and it increases rapidly thereafter – at an exponential rate (log or exponential phase). Here, both the progeny cells following mitotic cell division retain the ability to divide and continue to do so. However, with limited nutrient supply, the growth slows down leading to a stationary phase.

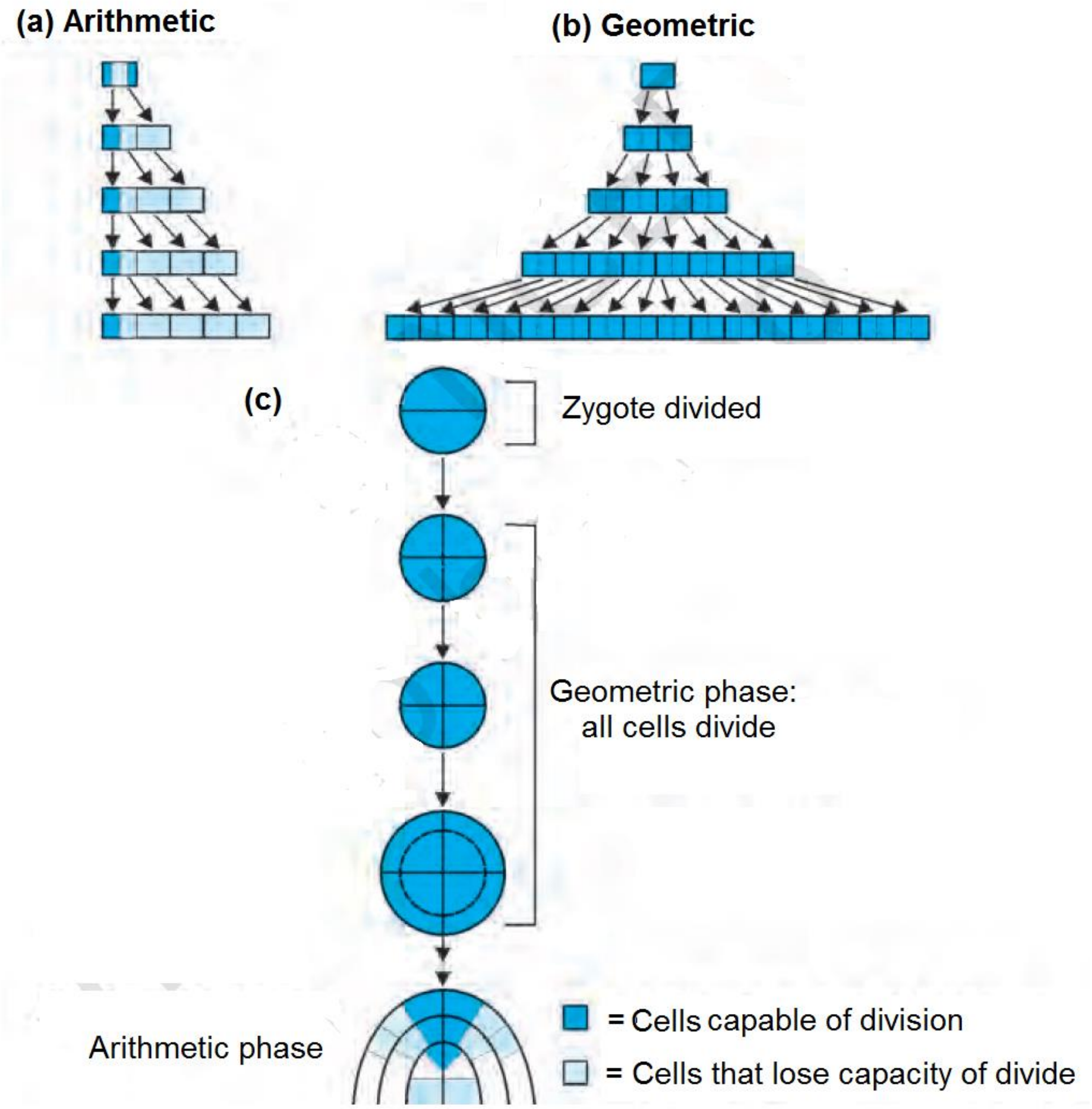


Figure 35 Diagrammatic representation of : (a) Arithmetic (b) Geometric growth and (c) Stages during embryo development showing geometric and arithematic phases

5.3. Growth rate measurement

Quantitative comparisons between the growth of living system can also be made in two ways : (i) measurement and the comparison of total growth per unit time is called the absolute growth rate. (ii) The growth of the given system per unit time expressed on a common basis, e.g., per unit initial parameter is called the relative growth rate. In **Figure 36** two leaves, A and B, are drawn that are of different sizes but shows absolute increase in area in the given time to give leaves, A1 and B1. However, one of them shows much higher relative growth rate.

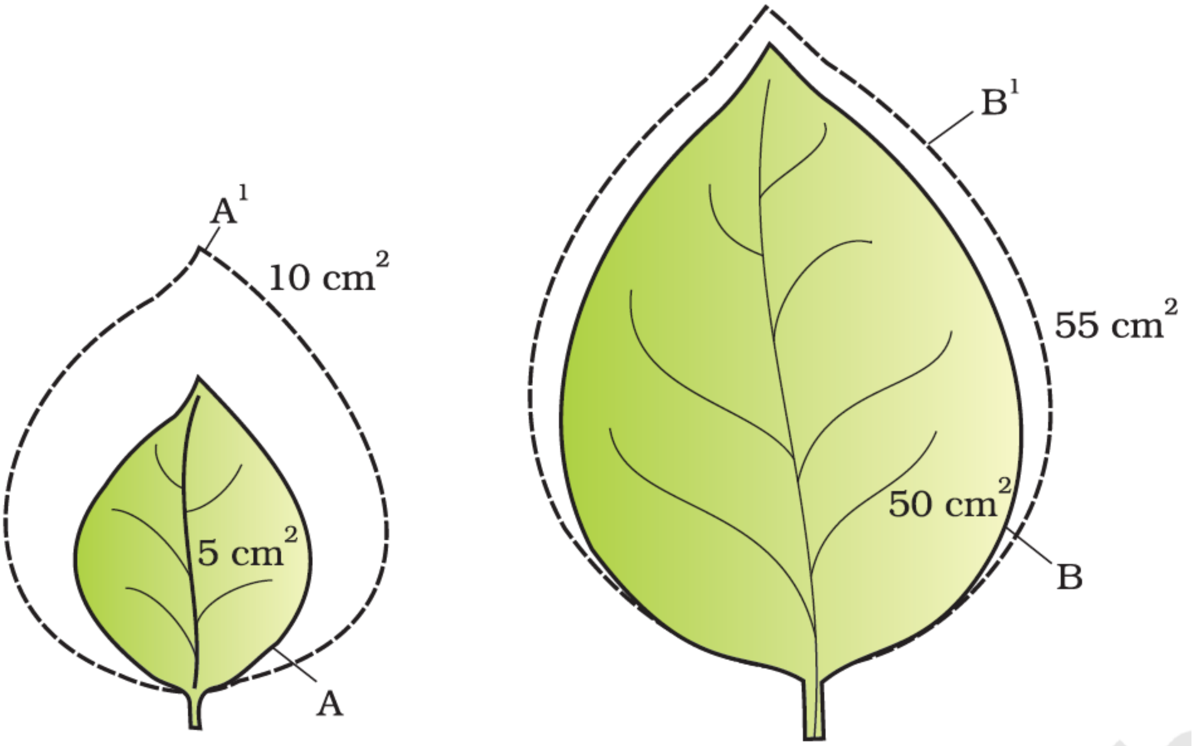


Figure 36 Diagrammatic comparison of absolute and relative growth rates. Both leaves A and B have increased their area by 5 cm^2 in a given time to produce A1, B1 leaves.

Glossary

Active transport—The movement of a molecule against its electrochemical gradient, requiring energy.

ADP (Adenosinediphosphate)—The lower-energy form of ATP, missing the third phosphate group.

Adsorption—The bonding of water molecules to tiny particles, generally by hydrogen bonding.

Agronomy—The science of farming.

Amino acids—The basic building blocks of proteins; nitrogen-rich compounds central to life.

Anion—A negatively charged ion.

Apical meristem—The growing point or generative structure that produces the plant body found at the tips of stems and branches.

Apoplast—The sum of all the plant body external to the cell membranes.

Aquaporins—Transmembrane channel proteins that allow the free passage of water.

Arbuscules—Highly branched profusions of hyphae formed inside the cell membrane of endomycorrhizae.

ATP (Adenosinetriphosphate)—The main energy carrier used in cellular metabolism.Most energy transfers using ATP involve the transfer of a phosphate group to or from the molecule.

Autotroph—An organism that fixes its own carbon using an energy source.

Bacteria—Simple single-celled organisms..

Bound water—The water adsorbed onto small soil particles unavailable for plant roots.

Carriers—Transmembrane proteins specialized to permit only certain molecules across the membrane in the direction of their electrochemical gradient, generally in concert with the movement of some other molecule.

Casparian strip—A waxy layer coating the sidewalls of the cortical cells immediately adjacent to the vascular cylinder of the root.

Cation exchange complex—The distribution of negative charges on the surfaces of soil particles typical in the temperate world, allowing nutrient exchange and increasing the nutrient holding capacity of the soil.

Cation—A positively charged ion.

Cell membrane—The phospholipid bilayer that envelops the cell and delimits the internal contents of the cell from the external environment.

Channels—Transmembrane proteins that allow the free movement of a molecule across the membrane along its electrochemical gradient.

Chlorophyll—The green, nitrogen-containing pigment that acts as the main light-harvesting compound in photosynthesis, with magnesium playing a central role in the physical structure of the molecule.

Chloroplast—A subcompartment of photosynthetic cells composed of cell membrane and containing proteins, chlorophyll, and other pigments; the site of photosynthesis in plants.

Chlorosis—A symptom of nutrient deficiency characterized by a yellowing of the leaves, generally between the veins.

Cortex—In a stem, the cells that are not part of the vascular system, exterior to the pith and interior to the epidermis. In a root, the cells between the vascular cylinder and the epidermis.

Electrochemical gradients—The combination of chemical and electrical concentration gradients responsible for predicting the direction of chemical movements by diffusion.

Embryo—The young, undeveloped plant in a seed.

Enzyme—A protein that exists to catalyze or facilitate a chemical reaction.

Epidermis—The outermost covering of the plant body in nonwoody plants.

Fixation—The process of making an inorganic compound, such as gaseous nitrogen or carbon dioxide, biologically available by chemically converting it to a different form.

Free water—The water of the soil solution not adsorbed to soil particles.

Fungi—Essentially microscopic organisms that have long, thin, thread-like bodies; also includes yeasts, which are single-celled, round fungi.

Hydrogen bond—A type of weak and sometimes transient chemical bond; critical to many aspects of biology.

Hydrophilic—Able to interact or mix with water; salt or sugar are hydrophilic.

Hydrophobic—Unable to interact or mix with water; oil and wax are hydrophobic.

Intracellular—Within the bounds of the cell membrane.

Leaf—A thin, flattened organ of the plant specialized for gas exchange and light capture for photosynthesis; the main photosynthetic organ of the plant body.

Legumes—A family of plants, Fabaceae, characterized by the formation of a pea-like or bean-like fruit; often associated with rhizobial root nodules.

Lignin—A plant cell wall compound that is highly resistant to most forms of biological degradation; provides the rigidity to the cell wall in tissues like wood.

Macronutrients—Essential plant nutrients required in relatively large amounts in plant tissues.

Mesophyll—The parenchymatous tissue between the epidermises of a leaf that is not a part of the vascular bundles.

Microbes—Microscopic organisms, such as bacteria, fungi, protists, and some animals.

Micronutrients—Essential mineral nutrients required by plants in relatively small amounts.

Nodules—Specialized round structures found on the roots of some plant species when colonized by nitrogen-fixing bacteria.

Nucleic acids—Nitrogen-containing molecules that form the basis for DNA and other information-carrying macromolecules in the cell.

Organelle—A membrane-bound entity inside a cell, generally with a specialized function.

Organic—Chemicals that are generally produced by living organisms and containing the element carbon.

Osmolyte—Solutes responsible for determining the water potential of the solution.

Osmotic pressure—The force generated by water flowing across a selectively permeable membrane in response to water potential.

Parenchyma—A type of cell in the plant body, alive at functional maturity and responsible for virtually all biochemical reactions.

Phloem—The tissue of the vascular system responsible for conducting dissolved sugars from areas of production, such as leaves, to areas of use, such as roots.

Phospholipids—Molecules with hydrophilic heads and hydrophobic tails that form the basis of cell membranes.

Photosynthate—The fixed carbon produced by photosynthesis; generally a sugar such as glucose.

Photosynthesis—The process by which light, water, and carbon dioxide are converted into sugar, oxygen, and water.

Protein—A complex molecule formed of amino acids; roles include enzymes, carriers, channels and pumps, and structural support.

Radicle—The first root produced by a seed as it germinates.

Respiration—The chemical process of extracting energy from sugar, used in some form by virtually all life on Earth.

Root apical meristem—The growing point of the root from which all root tissues are derived.

Root hair—The thin, cell wall outgrowth from a root epidermal cell in the vicinity of the zone of maturation in the root.

Stem—The rigid portion of the shoot responsible for holding aloft the leaves and conducting sap and photosynthate.

Stomata—The openings in the lower epidermis of the leaf that permit efficient gas exchange with the environment.

Transmembrane protein—A protein that spans from one side of the cell membrane to the other; generally involved in transport, signal transduction, or energy generation.

Transpiration—The process by which plant leaves lose water to the atmosphere, cooling them and providing the driving force for longdistance water movement in the plant.

Turgor—The pressure exerted on the cell wall by the cell membrane, keeping the herbaceous parts of the plant rigid.

Vascular system—The collection of all the vascular bundles and other vascular tissue throughout the plant.

Veins—The vascular bundles of leaves.

Vesicles—The balloon-like or spore-like structures formed inside plant cells by endomycorrhizal hyphae.

Water potential—The measurement of the potential energy of water in a given context; the predictor of water movement.

Xylem—The water- or sap-conducting tissue of the vascular system.

Yield—The amount of crop harvested at the end of the growing season.

Zone of cell division—The region of the root just behind the root apical meristem where the cells actively divide.

Zone of cell elongation—The region of the root just behind the zone of cell division where the cells actively elongate and push the root through the soil.

Zone of cell maturation—The region of the root just behind the zone of cell elongation where root hairs begin to form; this area of the root is responsible for the bulk of the nutrient and water uptake in the plant.

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