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Plant Physiology
Part 1: Physiology of Nutrition

This handout is designed for second-year Common Core students, third-year undergraduate students in Biology and Plant Physiology, and students specializing in Plant Biotechnology.

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Preface

Target audience: This plant physiology course booklet is intended for second-year students in the common core of Biological Sciences, third-year undergraduate students in Plant Biology and Physiology, as well as students in Plant Biotechnology.

Total workload: 35 hours of lectures and 12 hours of practical sessions.

Prerequisites: Students should have acquired knowledge in Plant Biology (structure and reproduction), General Biochemistry (primary and secondary metabolism, growth regulators), basic concepts of Botany, Molecular Biology (DNA, proteins), and basic notions of Ecology (biogeography, bioclimate).

Course objectives: The aim of this course is to enable students to:

- Understand the **fundamental principles** governing the functioning of plants at different levels of organization (cellular, tissue, organ, and whole-plant levels).
- Explain the **physiological mechanisms** that allow plants to grow, develop, reproduce, and adapt to various biotic and abiotic constraints.
- Connect knowledge of plant physiology to practical applications in **agriculture**, **horticulture**, **forestry**, and **biotechnology**.

This course covers the first part of the ‘Plant Physiology’ syllabus, which focuses on ‘Nutrition Physiology’. The second part, dealing with ‘Growth and Development’, will be addressed in a subsequent booklet.

Plant Physiology

Part 1: Physiology of Nutrition

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Plant Physiology

Part 1: Physiology of Nutrition

Introduction to Plant Physiology

Plant physiology is a central discipline within the biological sciences that studies how plants function, from the cellular level to the whole organism. Its aim is to understand the mechanisms that govern plant life, including how plants grow, develop, obtain nutrients, interact with their environment, and reproduce.

Unlike animals, plants are autotrophic organisms: they produce their own organic matter from mineral substances, mainly through photosynthesis. This fundamental process allows them to capture solar energy and convert it into chemical energy, while playing a key role in maintaining the planet's ecological balance, particularly in the carbon cycle and oxygen production.

The study of plant physiology requires an in-depth understanding of the structural organization of plants, which is based on a modular architecture comprising two main systems: the shoot system and the root system. Each of these systems consists of organs, which in turn are made up of specialized tissues that perform precise and complementary functions in the plant's overall operation.

Moreover, the physiological functions of plants are organized around two main groups of fundamental processes: nutrition and development. All these phenomena are finely regulated by internal factors (such as genetic and hormonal controls) as well as external factors (including light, temperature, water availability, and gravity).

Thus, plant physiology provides the essential foundations for understanding plant behavior in their environment and addresses a wide range of issues, whether agricultural, ecological, or biotechnological. It is a vital cornerstone for any training in plant biology and paves the way for better utilization of plant resources in the context of sustainable development.

Reminder Concept

1. The Classification of Living Organisms

Historically, living organisms were divided into two distinct domains: the prokaryotes (for example, the bacterial kingdom) and the eukaryotes (such as the plant kingdom). However, current phylogenetic classification has confirmed the concept of the unity of life: all present-day living organisms descend from a common ancestor known as LUCA (Last Universal Common Ancestor) (**Fig. 1**).

They are divided into three major groups, called domains:

1. Archaea (Archaebacteria)
2. Bacteria (Eubacteria)
3. Eukaryotes

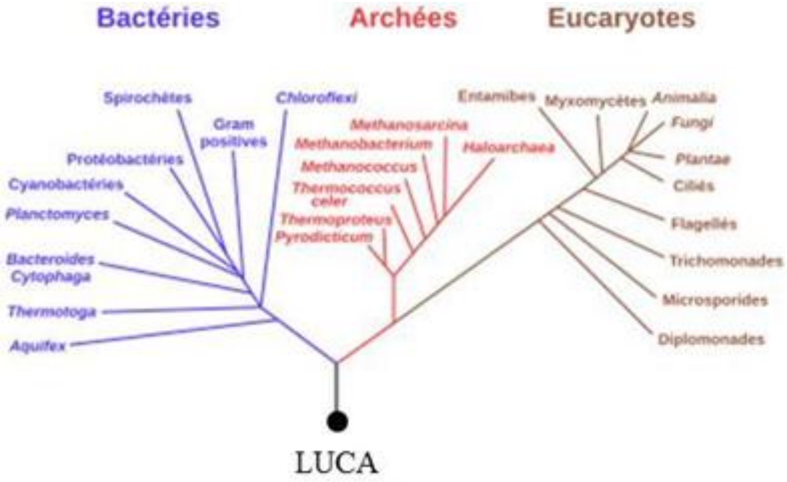


Figure 1. Phylogenetic tree of life.
LUCA: Last Universal Common Ancestor
(Woese et al., 1990)

The domain of prokaryotes is represented by the kingdom Monera, which is divided into two major groups:

- **Archaea:** Discovered relatively recently, these unicellular organisms lack a nucleus and are often extremophiles. They can survive and thrive in harsh environments such as salt marshes, hydrothermal vents, or even polar glaciers.
- **Eubacteria:** This group also includes unicellular organisms without a nucleus, many of which resemble the bacteria we encounter in everyday life, such as *Escherichia coli*.

The domain of Eukaryotes is subdivided into four kingdoms, according to Linnaeus's classification system:

- **Protozoa**
- **Animals (Animalia)**
- **Plants (Plantae)**
- **Fungi (Fungi)**

2. Organization of a Plant

Plants (*Plantae*) are essential organisms within the food chain and represent one of the major kingdoms in the domain of eukaryotes. To date, more than 400,000 plant species have been described, the vast majority of which — 341,526 species — are flowering plants, according to data from World Flora Online (WFO, 2023).

Specific Features of Plants

- ✓ **Autotrophic organisms:** They produce their own organic matter from inorganic substances (CO_2, H_2O) through photosynthesis.
- ✓ **Sessility:** They cannot move and must therefore adapt to their local environment.
- ✓ **Indeterminate growth:** They have the ability to grow throughout their entire lifespan.
- ✓ **Plasticity:** They exhibit morphological and functional adaptation to environmental conditions.
- ✓ **Low differentiation:** They have few tissue or organ types, which gives them a remarkable regenerative capacity and allows for vegetative propagation.

The plant kingdom is traditionally divided into two major groups based on structural organization:

1. **Thallophytes:** Plants without differentiated organs (no stem, leaves, or roots).
2. **Cormophytes:** Plants with well-differentiated organs (stems, leaves, and roots).

A plant's architecture includes two main systems (**Fig. 2**):

- The aerial system: Stem, leaves, flowers, fruits
- The underground system: Roots

The shape, size, color, and spatial organization of these systems determine the specific morphology of each plant.

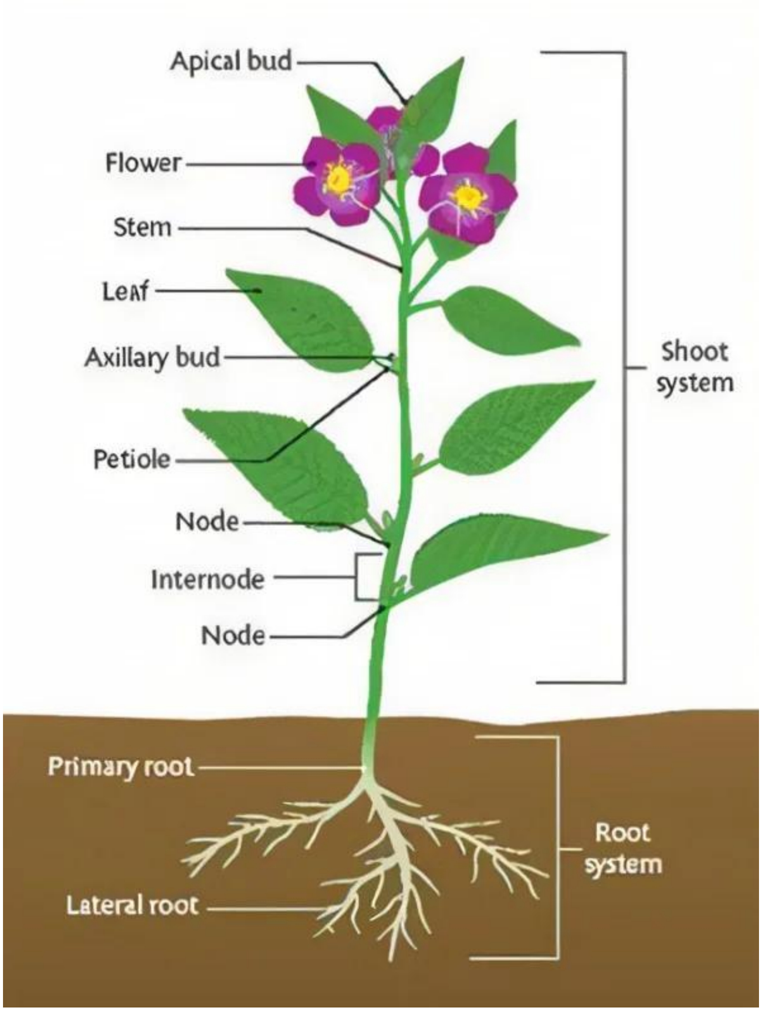


Figure 2. General structure of a flowering plant
wikipedia

2.1. The aerial system

The aerial system consists of the stem, an elongated organ that supports the leaves and flowers. Stems show a great diversity of shapes and textures, varying according to species and varieties.

The leaf is a lateral extension of the stem, composed of a flat part called the blade (lamina) and a thinner part, the petiole, which connects the blade to the stem. It performs several functions: respiration and transpiration (through the stomata), nutrition (via photosynthesis), storage of reserves (in succulent plants), vegetative reproduction (by cuttings), and sometimes defense (through the presence of spines).

The flower is a complex organ composed of various specialized parts: the calyx, the corolla, the androecium, and the gynoecium (**Fig. 3**). It contains the plant's reproductive organs and develops at the tip or in the axil of the stem. Flowering plants are thus capable of producing seeds and fruits.

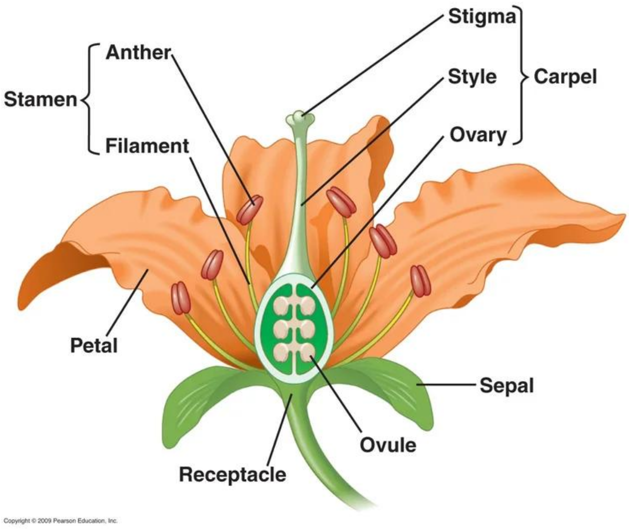


Figure 3. General structure of an angiosperm flower
(biofaculte.blogspot.com)

2.2. The underground system

The root is the underground part of the plant (**Fig. 4**).

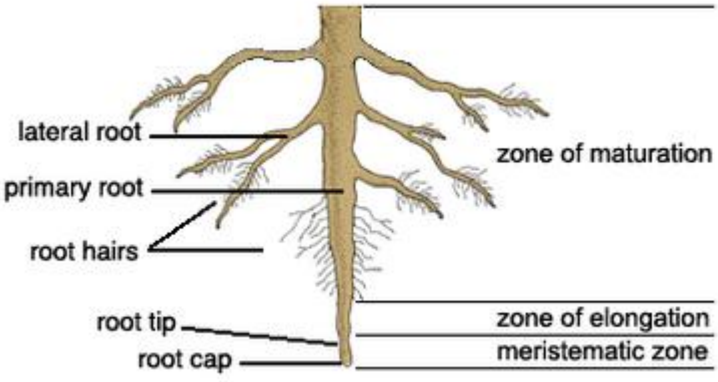


Figure 4. Root structure
(VanDerZanden, 2008)

It anchors the plant in the soil or onto a support, absorbs water and nutrients, and stores reserves (such as nutrients or air). Sometimes, it also contributes to reproduction. Roots can take various forms: fibrous or taproots, tuberous roots, adventitious roots, stilt roots, or aerial roots (pneumatophores). They can also transform into suckers or clinging organs (as in mistletoe or ivy).

3. Organization of a Plant Cell

Plant cells are the basic units that make up plant organisms. They generally include a cell nucleus surrounded by cytoplasm and various organelles, all enclosed by a cell membrane (**Fig. 5**). Their size ranges from 10 to 200 µm.

- **The pectocellulosic wall:** This rigid structure forms an external skeleton specific to plant cells, providing protection, support, and defining their size and shape.
- **Plasmodesmata:** These structures connect the cytoplasm of adjacent cells and allow exchange between them.

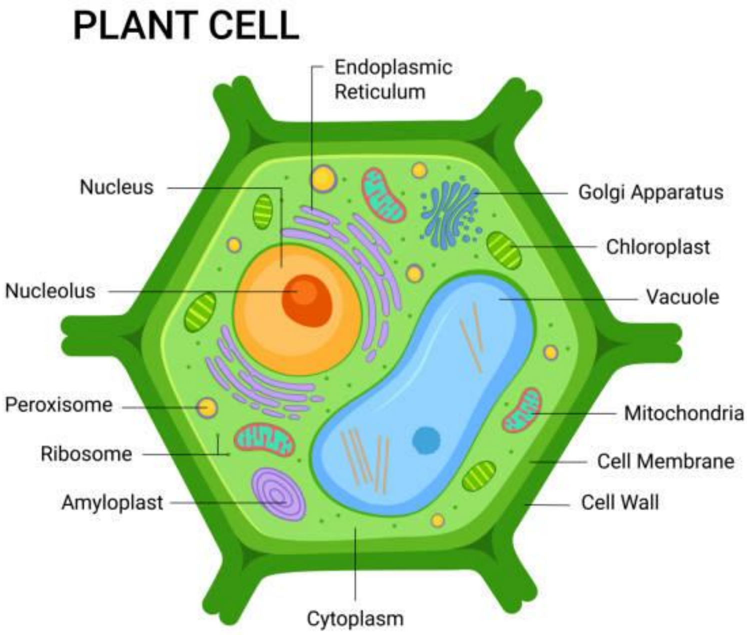


Figure 5. Structure of a plant cell
(Vitalii, 2019)

Inside the cell, there is the cytoplasm, enclosed by a plasma membrane, which contains several components:

- **The nucleus:** Surrounded by a nuclear membrane, it contains the genetic information.
- **Chloroplasts:** Organelles where photosynthesis takes place, found in the aerial parts of the plant and unique to the plant kingdom.
- **Mitochondria:** Responsible for converting the energy stored in organic molecules into usable energy (ATP) for the cell's functions.
- **Ribosomes:** Complexes of proteins and RNA that facilitate protein synthesis.
- **Endoplasmic reticulum:** The site of protein synthesis.
- **Vacuoles:** Specific to plant cells, they store water, ions, sugars, nitrogenous compounds, and waste products, occupying 80 to 90% of the cell volume.

3.2. Types of Plant Cells

Parenchyma

- Thin primary wall, no secondary wall.
- Carries out most metabolic functions, including synthesis and photosynthesis.
- Can accumulate reserves (carbohydrates, lipids, proteins).

Collenchyma

- Thick and strong primary wall, no secondary wall.
- Provides support for growing aerial parts, such as young stems (elastic and flexible).

Sclerenchyma

- Thick, rigid secondary wall impregnated with lignin.
- Generally composed of dead, rigid cells that cannot grow.
- Provides support to parts of the plant that are no longer growing.
- Forms bundles known as plant fibers.

Tracheids and Vessel Elements

- Ensure the transport of raw sap (water and minerals).
- Cells die at maturity.

Sieve Cells and Companion Cells

- Sieve cells allow the transport of processed sap (photosynthates).

4. Types of Plant Tissues

The three main classes of cells can differentiate to form the tissue structures of roots, stems, and leaves. These types of plant cells are classified according to the structure of their cell walls and the characteristics of their protoplasts, which determine their function.

- ✓ **Dermal tissues:** Outer covering of the plant (epidermis, cuticle).
    - Protection
    - Absorption (e.g., root hairs)
- ✓ **Vascular tissues:** Responsible for transporting substances throughout the plant.
    - **Xylem:** Transports raw sap (water and minerals) from the roots. Composed of tracheids, vessel elements, and fibers (sclerenchyma).
    - **Phloem:** Transports the products of photosynthesis (processed sap). Composed of sieve cells and companion cells.
- ✓ **Ground tissues :**
    - **Assimilatory tissue (parenchyma)**: ensures photosynthesis and storage of reserve molecules (carbohydrates, lipids, proteins)
- ✓ **Support tissues :**
    - Collenchyma
    - Sclerenchyma
- ✓ **Meristematic tissues:** Embryonic tissues responsible for plant growth.

Part I: Physiology of Nutrition

Chapter 1: Water in the Plant

I. Water Nutrition

Water is an essential element for the survival of plants, playing several crucial roles. It is involved not only in supplying the mineral salts necessary for nutrition but also in hydrating cells and maintaining water potential, turgor pressure, and osmotic balance.

The concept of water nutrition covers several aspects, including the soil, the plants, and the atmosphere.

I.1 Water Reservoirs

I.1.1. Water in the Soil

The water present in the soil comes from natural precipitation or artificial irrigation. Part of this water runs off the surface before infiltrating the soil, where it is distributed in different forms (**Fig. 6**):

- **Constitution water:** Integrated into the chemical and mineral structure of certain minerals, especially clays.
- **Adsorbed water:** Tightly bound to the surface of soil particles.
- **Capillary water:** Held in the fine pores of the soil by surface tension forces.
- **Free water:** Moves through the soil pores under the influence of gravity.

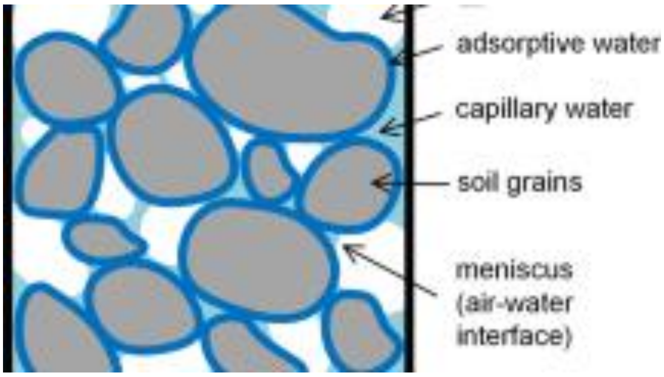


Figure 6. Forms of water in the soil

Soil water is subject to several forces of varying magnitudes, which influence its availability to plants:

- **Gravity:** The force that causes water to flow deeper into the soil.
- **Osmotic forces:** Attractions exerted on water by ions dissolved in the soil solution.
- **Imbibition forces:** Electrostatic interactions between the negative charges of soil colloids and water molecules.
- **Capillary forces:** Surface tension forces that hold water in the soil’s micropores.

Osmotic, imbibition, and capillary forces are collectively referred to as retention forces, as they determine the amount of water available to plants.

I.1.2. Water in the Plant

Water is a fundamental component of living matter. It is mostly present in liquid form but also exists as vapor in the intercellular spaces and the substomatal chambers of leaves. In plants, water is distributed in three main forms:

- **Constitution water:** Integrated into organic molecules, it accounts for about 3 to 4% of the total water content in the plant.
- **Imbibed (bound) water:** Held by the hydrophilic colloids of the cells, it makes up about 20% of the total water.
- **Free water:** Located in the pectocellulosic walls, intercellular spaces, vacuoles, and conducting vessels. This water plays an essential role in the transport of nutrients and minerals, as well as in maintaining turgor pressure.

I.2. Water Absorption by Roots

Water absorption by roots is a fundamental process for the survival and growth of plants. In addition to taking up water from the soil, roots play a crucial role in absorbing the nutrients needed for plant development.

Roots consist of different zones, each with a specific function. The root apex, or root tip, is responsible for growth and soil exploration. Just behind this zone, over a length of about 10 cm, is the region of maximum water absorption. This region corresponds to the zone of cell differentiation, where the conducting tissues begin to specialize. It is also in this area that root hairs actively develop.

Root hairs are extensions of epidermal cells with thin walls that greatly increase the absorption surface area. They enable the roots to explore a larger soil volume (**Fig. 7**).

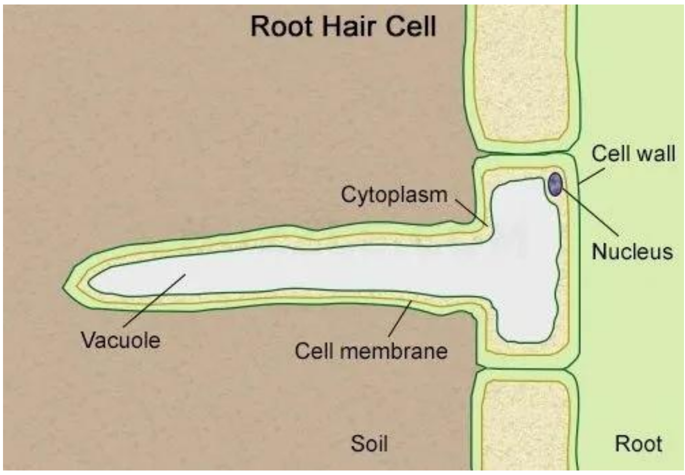


Figure 7. Root hair
(Grierson C. & Schiefelbein J., 2002)

With an average diameter of about 10 µm, these root hairs can measure from 0.1 to 10 mm depending on the species and environmental conditions. They form a dense fuzz, visible to the naked eye, located just behind the root apex. A single root tip can bear up to 2,500 root hairs per cm², thus increasing the absorption surface area of the root by a factor of 1.5 to 20.

Their small diameter allows them to explore the soil's micropores, which are inaccessible to the main roots, thereby maximizing contact with water and nutrients.

However, root hairs have a short lifespan, lasting only a few days to a few weeks. They are continuously renewed as the root grows. Their disappearance can be accelerated by unfavorable conditions such as excessive soil acidity or lack of oxygen.

Root hairs do not possess specific absorption mechanisms but have morphological characteristics that are particularly favorable for water exchange:

- Very thin pectocellulosic wall, facilitating the passage of water.
- Large vacuoles, playing a key role in osmotic regulation.
- Considerable contact surface area, improving absorption efficiency.

Thanks to these adaptations, root hairs form an essential interface between the soil and the plant, enabling efficient absorption of water and nutrients, which are vital for plant growth and metabolism.

I.3. Mechanisms of Water Absorption

The main mechanism for water entry into the plant relies on physico-chemical laws. Water absorption is a passive process, in the thermodynamic sense, resulting from the difference between the water potential of the root hair and that of the soil.

Concept of Osmotic Pressure

The vacuolar fluid of a plant cell has a certain osmotic pressure, described by the following equation:

$$Po = R \cdot T \cdot C$$

- **Po:** atmospheric osmotic pressure
- **R:** ideal gas constant
- **T:** absolute temperature
- **C:** molar concentration of the vacuolar fluid

Cellular Mechanisms of Absorption in Roots

Water exchange between the intracellular and extracellular environments occurs according to the physical laws of diffusion, specifically by osmosis. This phenomenon corresponds to the diffusion of water through a semi-permeable membrane, moving from the less concentrated medium (hypotonic) to the more concentrated medium (hypertonic).

The osmotic pressure that determines the water flow is proportional to the concentration difference between the two media. Thus, a cell placed in a hypertonic solution loses water and becomes plasmolyzed. Conversely, if it is in a hypotonic medium, water enters the cell, causing the vacuole to swell and making the cell turgid (**Fig. 8**).

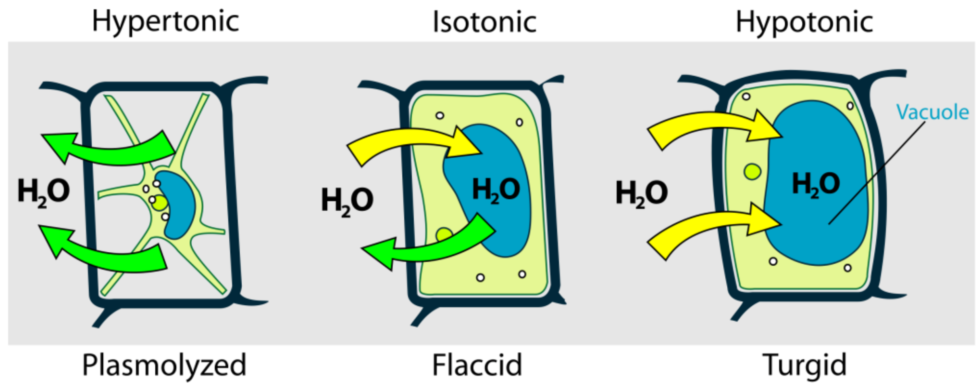


Figure 8. Turgor and plasmolysis of a plant cell (Villarreal, 2007)

Under natural conditions, the cells of root hairs (or those of mycorrhizae) are always hypertonic compared to the soil solution, which allows them to absorb water passively through osmosis.

Concept of Water Potential

The water in the vacuoles forms a solution of mineral salts and metabolites, generating an osmotic pressure (**Po**) that draws water from the outside into the cell. However, the cell walls and membranes resist the expansion of the cell contents by exerting an opposing wall pressure (**Pm**).

As water enters the cell, the osmotic value decreases due to dilution of the solution, while the wall pressure increases. Eventually, an equilibrium is reached between the two pressures (**Po = Pm**), and no more water enters. This difference between the two opposing pressures is called the **suction force** or **water potential (Ph)**. It is defined as a thermodynamic quantity that makes it possible to predict water movement.

$$Ph = Po - Pm$$

I.4. Factors Controlling Water Absorption by Roots

Water absorption is closely linked to the plant's physiological activity; however, it also depends on external factors that influence the soil's water potential and the roots' ability to take up water.

I.4.1. Climatic Factors

- **Air temperature and humidity:** These factors indirectly affect absorption by changing the amount of water lost through transpiration.
- **Soil temperature:** A decrease in soil temperature reduces water absorption.
- **Wind:** Increases transpiration, creating a greater water demand.
- **Light intensity:** Stimulates stomatal opening and promotes transpiration.

I.4.2. Pedological Factors

- **Soil structure and texture:** Sandy soil retains less water than clay soil.
- **Presence of mineral salts:** Excessive salinity reduces absorption by increasing osmotic stress.

I.5. Methods for Measuring Water Absorption by Roots

Several techniques can be used to assess water absorption by roots:

- By simple weighing
- Using a potometer (**Fig. 9**)

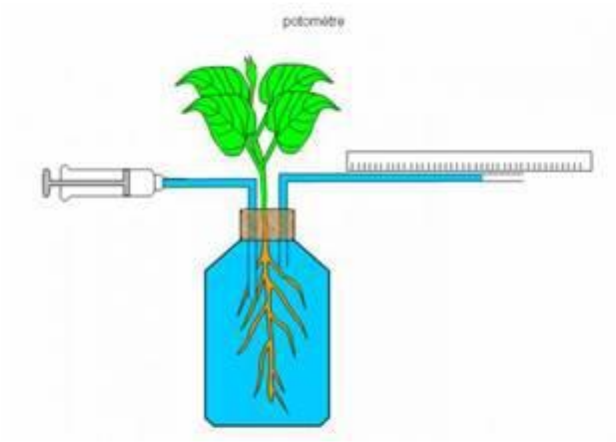


Figure 9. Vescque’s potometer

I.6. Water Transport in the Plant

The water absorbed must be transported to the aerial parts to ensure growth and transpiration.

I.6.1. Water Transport in the Roots

A cross-section taken at the root hair zone of a young root (**Fig. 10**) shows the presence of two clearly distinct concentric zones: the cortex and the central cylinder where the conducting vessels are located.

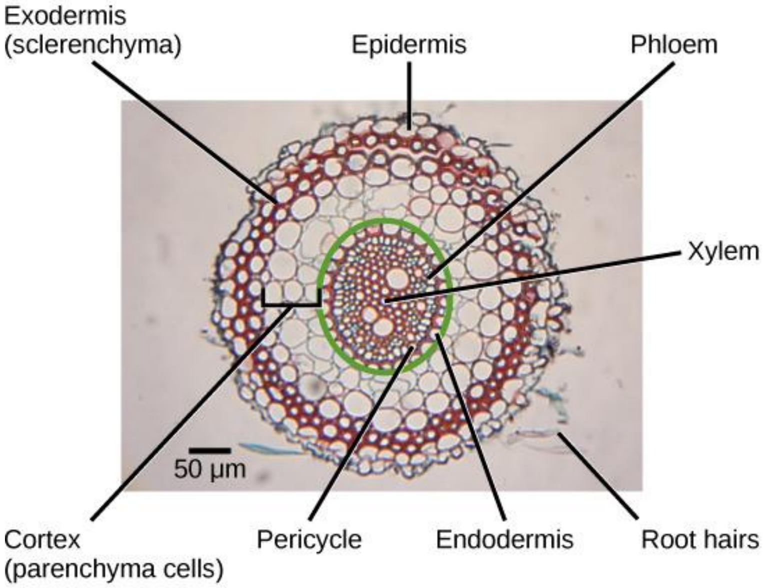


Figure 10. Cross-section at the root hair zone of a root
(https://oertx.highered.texas.gov/courseware/lesson/1767/overview)

Measurements of osmotic pressure taken on a root indicate the presence of an inversion of the osmotic pressure gradient at the endodermis (**Fig. 11**).

This inversion is a key phenomenon in the absorption of water and nutrients by plant roots.

From the root hairs to the endodermis, water moves passively according to the laws of osmosis. From the endodermis, transport becomes active. This process requires energy, often in the form of ATP, to move ions and other solutes against their concentration gradient.

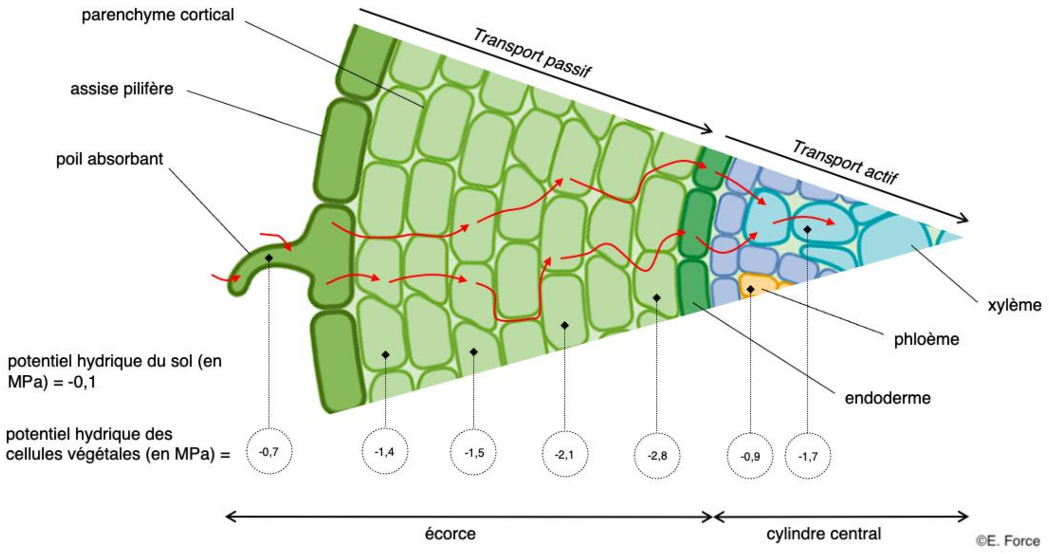


Figure 11. Root absorption and lateral water movement
Red arrows: pathway of water. (Force, 2021).

I.6.1.1. Water Pathways (Transport of Water to the Xylem Vessels)

Water is absorbed by the root hairs, crosses the cortex and the central cylinder, and reaches the conducting vessels. To do this, it follows three pathways (**Fig. 12**):

- **The apoplastic pathway:** This route uses the cell walls, intercellular spaces, and cavities. It is highly accessible for water and mineral ions.
- **The symplastic pathway:** This route uses the cytoplasm of the cells and the plasmodesmata at the pits to move from one cytoplasm to another.
- **The transcellular pathway (from vacuole to vacuole):** This route also uses the cytoplasm inside the plant cell but crosses the cell wall to move from one cytoplasm to the next.

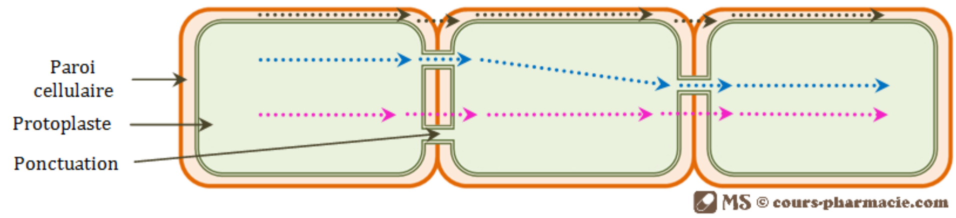


Schéma simplifié des voies utilisées par l'eau pour se rendre des radicelles aux vaisseaux de xylème (vaisseaux de bois) : voie transcellulaire, voie symplastique et voie apoplastique.

Figure 12. Water transport pathways in plant cells (Simon, 2009)

I.6.1.2. Root Pressure:

At the entry point to the vessels, water is released under pressure; this is known as **root pressure**, which often exceeds 1 bar (**Fig. 13**).

(Maple: 1 bar, grapevine: 1.25 bars, birch: 2 to 2.5 bars)

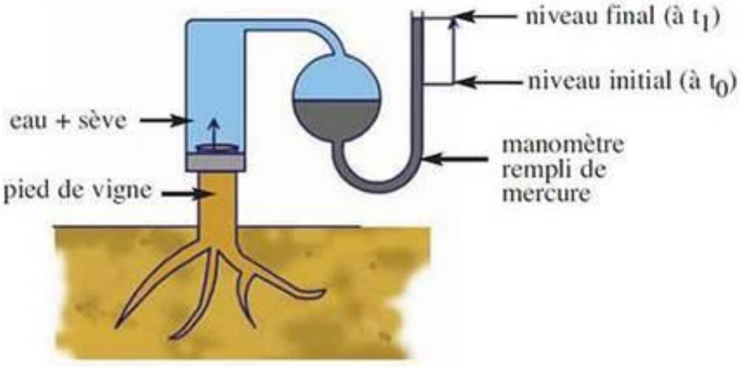


Figure 13. Root pressure (Hales' experiment, 1727)

Root pressure is an important phenomenon in plant functioning, especially regarding the upward movement of sap in the roots. It results from the metabolic activity of root cells, which creates positive pressure within the xylem.

This mechanism begins with water absorption by the roots, which causes dilution of solutes within the root cells. Water, rich in dissolved nutrients, enters the cells by osmosis. As the cells fill with water, the internal pressure increases, generating root pressure.

This pressure pushes water and nutrients upward through the xylem, allowing their distribution throughout the plant. Although root pressure is not the main mechanism for sap ascent (this role is primarily fulfilled by transpiration), it plays a crucial role, especially during periods of low transpiration (such as at night) or during water stress.

Root pressure is also influenced by external factors, such as soil temperature and moisture.

I.6.2. Water Transport in the Stem

Characteristics:

The mineral solution coming from the cortex and collected in the vessels forms the **raw sap**, which is a very dilute solution of mineral salts (0.1 to 2 g/l) with an osmotic pressure of at least 1 bar. By the end of its journey, it becomes depleted in mineral salts but enriched with organic substances.

Mechanisms:

The movement of water through the stem is a fundamental process for plant survival and growth. This phenomenon, known as **conduction**, occurs mainly in the **xylem**, a specialized vascular tissue that transports water and nutrients from the roots to the leaves.

When the roots absorb water from the soil, it enters the xylem by osmosis. The water, enriched with minerals, generates a positive pressure that helps push this flow upward through the plant. This phenomenon is called **root pressure**.

Root pressure is a key component of the water transport system, working in synergy with two main mechanisms to ensure the efficient and continuous circulation of vital resources: **transpiration** and **water cohesion**.

Transpiration, which occurs mainly through the stomata of the leaves, generates a tension that pulls water upward. Cohesion allows water molecules to attract each other, forming a continuous column within the xylem.

This transport is vital because water not only acts as a solvent for nutrients but also plays a crucial role in photosynthesis, plant cooling, and maintaining cell structure. The stem, as the main conduit, ensures that every part of the plant receives the necessary moisture to thrive.

II. Transpiration and Water Balance

Transpiration is the process by which plants lose water in the form of vapor, mainly through the stomata of the leaves.

II.1. Demonstration and Measurement of Transpiration

Plant transpiration can be demonstrated and quantified through various experiments. It corresponds to the amount of water released per unit of time and per unit of mass (or surface area) of the transpiring material.

- **Plastic bag experiment:** By enclosing a plant in a transparent plastic bag, condensation forms due to the water vapor released by the plant.
- **Weighing a potted plant that is not watered, or a detached organ:** By measuring the loss in weight over a given period, one can estimate the amount of water transpired.
- **Using a potometer:** This device indirectly measures transpiration by evaluating the water uptake by a plant.
- **Absorption of released water using a hygroscopic agent:** Substances such as calcium chloride ($CaCl_2$) or phosphorus trioxide (P_2O_5) can absorb the transpired water, allowing its measurement.

II.2. Location of Transpiration in the Plant

Transpiration occurs mainly in the leaves, specifically through:

- **Stomata:** These are pores located on the leaf epidermis and account for the majority of transpiration, representing about 90% of water loss.
- **Cuticle:** This waxy layer limits water loss but allows some transpiration when it is very thin.
- **Lenticels:** Found mainly on stems and some fruits, these structures enable gas exchange and contribute to transpiration, though to a much lesser extent.

II.2.1. Stomata

Stomata are specific anatomical structures located on the leaf epidermis (**Fig. 14**). They consist of two kidney-shaped, opposing guard cells that surround an opening called the **stoma** or **pore**. Beneath these cells is a large cavity, the **sub-stomatal chamber**, which plays an essential role in gas exchange and the regulation of transpiration.

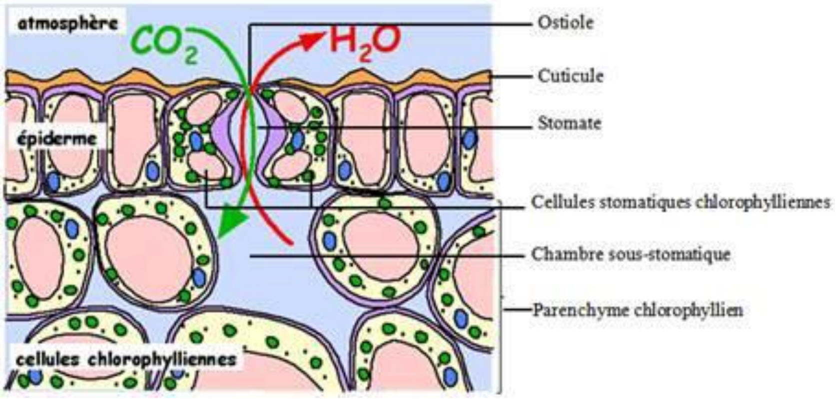


Figure 14. Longitudinal section through the chlorophyllous parenchyma
(Prat, 2005)

II.2.2. Mechanisms of Stomatal Opening

The guard cells have thickened inner walls bordering the stoma. This morphological feature indicates that the opening of the stomata results from a mechanical deformation of the guard cells, induced by vacuolar pressure (**Fig. 15**).

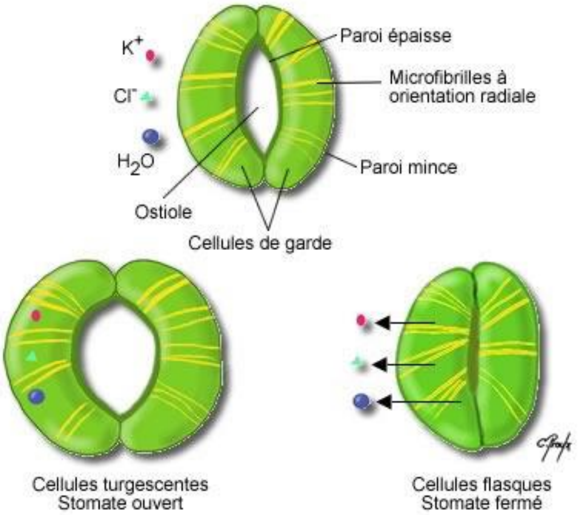


Figure 15. Diagram of a stoma
(Saugier, 2019)

The opening and closing of stomata are regulated by osmotic variations, mainly related to the intracellular concentration of potassium ions (K^+). When this concentration increases, an osmotic gradient is created, causing water to flow into the guard cells. This results in their turgidity and, consequently, the opening of the stomata.

Conversely, when the potassium concentration decreases, water exits the cells, causing them to plasmolyze and leading to the closing of the stomata.

II.3. Factors Influencing Transpiration

II.3.1. Plant-Related Factors

Stomatal transpiration depends on the plant's anatomy, particularly the evaporation surface (leaf surface area, cuticle thickness, distribution and density of stomata).

II.3.2. Environmental Factors

Stomatal transpiration also depends on environmental factors (soil type, soil water availability, air humidity, air movement, temperature, light intensity).

II.4. Physiological Regulation of Transpiration

Transpiration is a process regulated by various physiological mechanisms, which allow it to optimize gas exchange while limiting water loss, thus ensuring a balance between photosynthesis and water conservation.

II.4.1. Mechanism of Stomatal Opening and Closing

The opening and closing of stomata are controlled by the guard cells, which swell or shrink in response to changes in the plant's water status and environmental stimuli.

II.4.2. Factors Influencing Stomatal Opening

Several external and internal factors influence the opening and closing of stomata:

- Light
- CO_2 concentration
- The plant's water status

II.4.3. Role of Plant Hormones in Stomatal Regulation

Plant hormones play a key role in modulating stomatal opening and closing, particularly in response to environmental variations:

- ✓ **Abscisic acid (ABA):**

  This stress hormone acts by stimulating the release of K^+ ions from the guard cells, causing them to plasmolyze and the stomata to close quickly, which limits water loss.

- ✓ **Cytokinins:**

  These hormones promote stomatal opening when environmental conditions are favorable, mainly by stimulating water uptake by the guard cells.

II.5. Water Balance in Plants

Water is an essential element for the survival and development of plants. Its absorption, distribution, and loss are regulated by precise mechanisms that allow plants to maintain an optimal water balance, even under challenging environmental conditions. This balance relies on the concept of **water potential** and on various adaptation strategies developed by plants to cope with fluctuations in water availability.

II.5.1. Concept of Water Potential

Water potential (Ψ) helps explain the dynamics of water movement within the plant. Water always moves from an area of higher water potential to an area of lower water potential.

- In the roots, the water potential is relatively high, which promotes water absorption from the soil.
- Water then moves upward through the xylem toward the aerial parts of the plant, driven by transpiration and the cohesion of water molecules.
- In the leaves, water evaporates through the stomata into the atmosphere, where the water potential is very low.

II.5.2. Adaptation Strategies to Water Conditions

The water balance of plants is a key factor for their survival and growth. Thanks to a gradient of water potential, water moves continuously through the plant, enabling nutrient transport and temperature regulation. In response to variations in water availability, plants have developed several physiological and morphological strategies to maintain their water balance and limit water loss.

- **Closing stomata during drought:**
  In periods of water stress, some plants close their stomata to reduce water loss, although this also limits CO_2 uptake needed for photosynthesis.
- **Osmotic adjustment to maintain water absorption:**
  Osmotic adjustment is a mechanism by which plant cells accumulate compatible solutes (sugars, amino acids, K^+ ions) to lower their own water potential, allowing them to continue absorbing water despite a decrease in soil water potential. This mechanism is particularly important in drought-tolerant plants and halophytes (plants living in saline environments).
- **Development of deep root systems:**
  Some plants adapted to arid environments have very deep roots capable of reaching underground water tables (e.g., Acacia).

II.6. Importance of Transpiration for the Plant

The importance of transpiration for plants is multifaceted:

1. **Ascent and circulation of raw sap:**

   Transpiration generates a suction force that enables the ascent and circulation of raw sap within the xylem.

2. **Thermal regulation and nutrient transport:**

   Transpiration allows the plant to cool its leaf surface and avoid overheating. It also facilitates the transfer of mineral salts to the parts of the plant that need them most, mainly the leaves where photosynthesis occurs.

3. **Maintenance of cell turgor:**

   Essential for keeping tissues rigid and preventing wilting.

4. **Gas emission and communication:**

   Along with water vapor, the plant also releases gases, mainly oxygen, as well as aerosols containing phytohormones. These compounds allow the plant to communicate with other plants and to send “chemical messages” detectable by certain animals, especially insects.

Chapter 2: Mineral Nutrition in Plants

Plants are described as autotrophic organisms because they synthesize all of their organic matter from elements they extract from the environment in mineral form. In this way, they serve as the main entry point for minerals into food chains, ensuring that consumers receive essential nutrients.

Mineral nutrition refers to the uptake and use of chemical elements (other than carbon, oxygen, and hydrogen) that are necessary for the growth and development of plants. These elements are mainly absorbed by the roots in the form of ions dissolved in the soil solution.

I. Plants' Requirements for Mineral Elements

As autotrophic organisms, plants have specific nutritional requirements to ensure their growth, development, and reproduction. These needs are met through the absorption of various mineral elements, which are indispensable for physiological and biochemical processes.

I.1. Essential Nutrients

Elements required for plant growth and development are called *essential elements*. This classification is based on two criteria:

(a) An element is considered essential if its absence prevents the plant from completing its full life cycle.

(b) An element is essential if it forms part of a constituent or metabolite that is indispensable to plant metabolism.

Essential elements are divided into two categories: macronutrients and micronutrients (or trace elements).

I.1.1. Macronutrients

Macronutrients play a fundamental role in the structure and functioning of plant cells. Because they are involved in major biological processes, they must be supplied in relatively large amounts (more than 10 mmol/kg of dry matter).

There are two types of macronutrients:

- **Primary macronutrients:** These are elements that plants need in large amounts and continuously. They include Nitrogen (N), Phosphorus (P), and Potassium (K).
- **Secondary macronutrients:** These are needed in smaller quantities and at specific stages of the plant's life cycle. They include Sulfur (S), Calcium (Ca), and Magnesium (Mg).
- In addition, three other elements essential to plant life are obtained directly from water and air: Carbon (C), Hydrogen (H), and Oxygen (O).

I.1.2. Micronutrients (Trace Elements)

These are also required but in much smaller quantities: Iron (Fe), Zinc (Zn), Copper (Cu), Boron (B), Manganese (Mn), Silicon (Si), Molybdenum (Mo), Sodium (Na), Cobalt (Co), and Chlorine (Cl). These micronutrients occur in very small amounts in the soil and in plants (not exceeding 0.01% of the dry matter). However, their roles are just as vital as those of macronutrients.

I.2. Nutritional Status of Plants

The nutritional status of a plant largely depends on the availability of mineral elements in the soil. Several nutritional states can be distinguished:

- **Deficiency state:** One or more mineral elements are present in insufficient amounts, leading to specific symptoms such as leaf yellowing (*chlorosis*), stunted growth, or overall weakening. The most common deficiencies involve Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca), Magnesium (Mg), and Iron (Fe).
- **Sufficiency state:** The plant receives all the necessary mineral elements in adequate quantities, allowing it to achieve optimal growth and development.
- **Imbalance state:** Uneven uptake of certain elements can disrupt the assimilation of other minerals, leading to negative effects on plant health.
- **Excess state:** An excessively high concentration of a mineral element can be toxic and harm the plant’s growth and metabolism.

I.3. Sources of Mineral Elements

The mineral supply for plants depends on several natural and human-related sources:

- ✓ **Weathering of parent rock:** Gradually releases minerals into the soil, making them available to plants.
- ✓ **Decomposition of organic matter:** Decomposer organisms break down plant and animal residues into nutrients that plants can absorb.
- ✓ **Agricultural practices:** The application of fertilizers enriches the soil with nutrients and compensates for losses caused by harvesting and leaching.

II. Transport of Elements within the Plant

The transport of mineral elements in plants is an essential process for their growth and development. This complex mechanism begins with the absorption of ions by the roots and continues through various transport pathways.

II.1. Ion Absorption by the Roots

Roots play a crucial role in absorbing mineral elements dissolved in the soil. This process occurs mainly at the interface between the roots and the surrounding soil. Mineral elements are absorbed in ionic form, with anions generally being absorbed at a slower rate than cations.

The rate of ion absorption varies depending on several factors, including the plant species, its age, the type of root cells, the mineral composition of the soil, and the physiological condition of the cells. These factors influence the roots' ability to capture the nutrients needed for the plant's growth and development.

II.2. Radial Movement of Ions in the Root

To reach the conducting tissues located at the center of the root (the stele), ions must move transversally across the root.

This movement follows three main pathways: the **apoplastic pathway**, the **symplastic pathway**, and the **transcellular pathway** (see **Fig. 13**).

At the level of the endodermis, elements can no longer use the apoplastic pathway due to the presence of the **Casparian strip**, a structure impregnated with suberin. They must then switch to the symplastic pathway before reaching the xylem.

II.3. Transport of Solutes Across Membranes

The transport of ions and solutes across cell membranes can be classified into two categories: **passive transport** and **active transport**.

II.3.1. Passive Transport

Passive transport is a diffusion process in which the direction of movement is determined by the concentration gradient or the electrochemical gradient. It does not require any direct input of metabolic energy.

II.3.1.1. Simple Diffusion

The cell membrane allows water and non-polar molecules, such as methane (CH_4), benzene (C_6H_6), and neon (Ne), to cross freely by simple diffusion (**Fig. 16**). Diffusion naturally moves toward equilibrium, seeking to eliminate the concentration gradient.

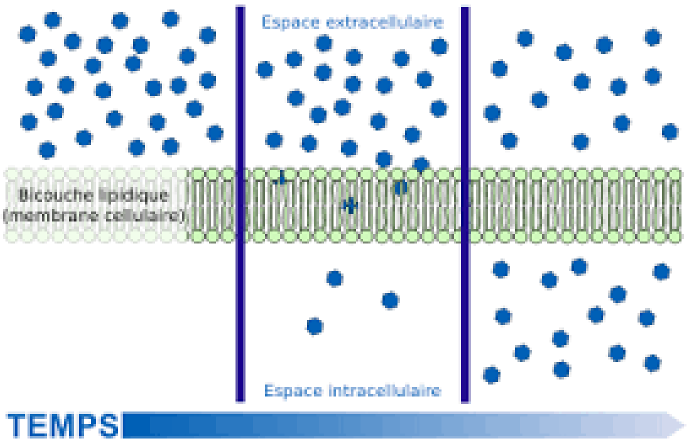


Figure 16. Simple Diffusion (Villarreal, 2010)

II.3.1.2. Facilitated Diffusion

Transport occurs along the concentration gradient and the electrochemical gradient. However, the molecules do not cross the membrane directly; instead, they must use a transmembrane transport protein (**Fig. 17**).

These proteins facilitate the passage of polar molecules and ions through the hydrophobic interior of the membrane.

Two types of proteins are distinguished:

- **Channel proteins (ion channels)**: These form water-filled pores that span the entire membrane and, when open, allow specific solutes (such as Na^+, K^+, Ca^{2+}, and Cl^-) to pass through. They do not change shape to permit passage.
- **Carrier proteins**: These bind to specific solutes and undergo conformational changes to transport the solutes across the membrane.

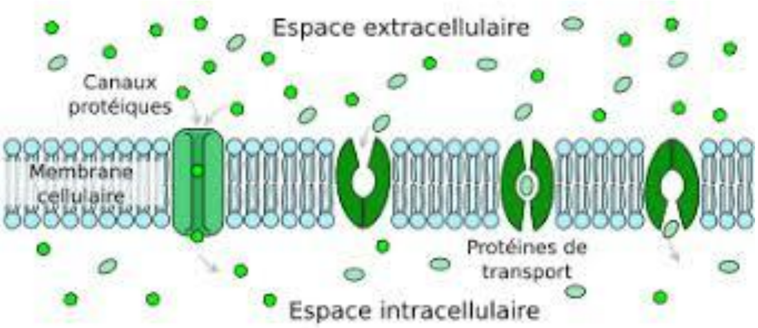


Figure 17. Facilitated Diffusion (Villarreal, 2007)

II.3.2. Active Transport

Active transport refers to the movement of an ion or molecule across a membrane *against* its concentration gradient, requiring an input of energy.

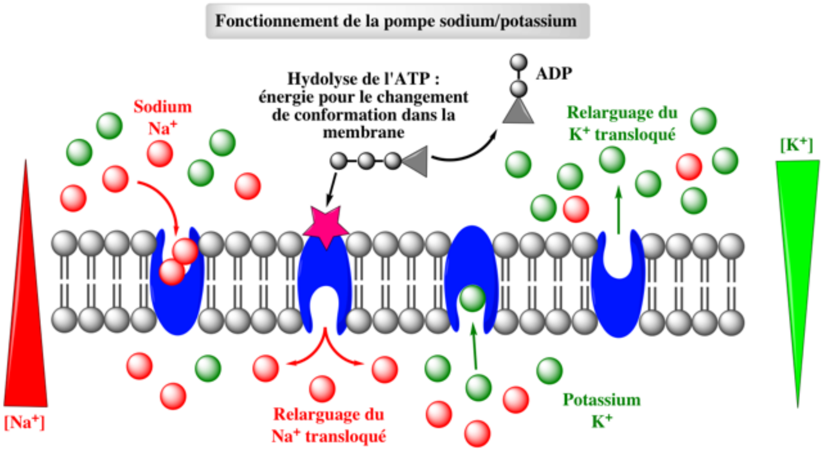
When particles must be transferred from a compartment with a low concentration to one with a higher concentration (i.e., against the gradient), an active transporter is needed to perform the transfer.

II.3.2.1. Primary (Direct) Active Transport

This type of transport uses energy directly from ATP hydrolysis to move molecules against their concentration gradient through the membrane (**Fig. 18**). It requires the involvement of transport proteins that act as membrane pumps. These pumps use chemical energy, usually in the form of ATP.

Examples:

- **Sodium-Potassium ATPase pump:** Expels 3 Na^+ ions out of the cell and brings in 2 K^+ ions.
- **Calcium ATPase pump:** Pumps Ca^{2+} ions out into the extracellular space.
- **Proton pump (H^+-ATPase):** Plays a key role in regulating cellular pH.
- **Molecule pumps:** Transport various compounds, including hormones.



E. Jaspard (2012)

Figure 18. Primary active transport (Na-K pump)

II.2.2. Secondary active transport (or coupled transport, cotransport)

This type of transport allows molecules to move in a direction opposite to their concentration gradient. Therefore, it requires an energy source, which is not directly provided by ATP but comes from the electrochemical gradient previously established by a primary active transport mechanism.

There are two main forms of secondary active transport: symport and antiport.

➤ **Antiport**

Two types of ions or solutes are transported simultaneously but in opposite directions across the membrane. One of these components naturally moves down its concentration gradient (from the compartment with higher concentration to the one with lower concentration), while the other is transported against its gradient.

A typical example is the sodium-calcium exchanger (Na^+/Ca^{2+}): this transporter uses the energy stored in the sodium electrochemical gradient (3 Na^+) to allow Na^+ to enter the cell along its gradient (**Fig. 19**) in exchange for the outward (antiport) transport of calcium ions (1 Ca^{2+}). This mechanism is essential for maintaining low calcium concentrations inside cells.

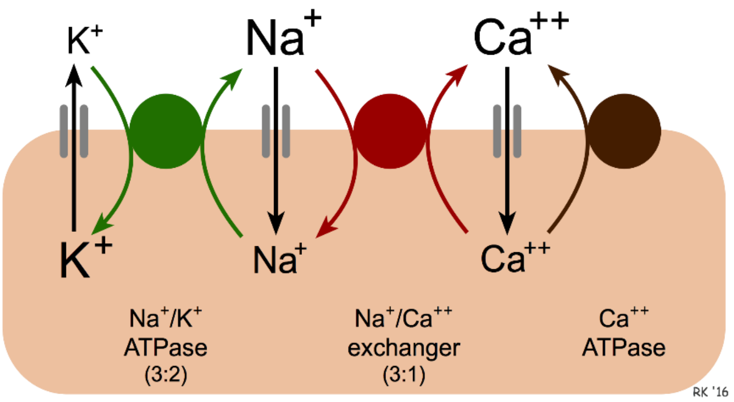
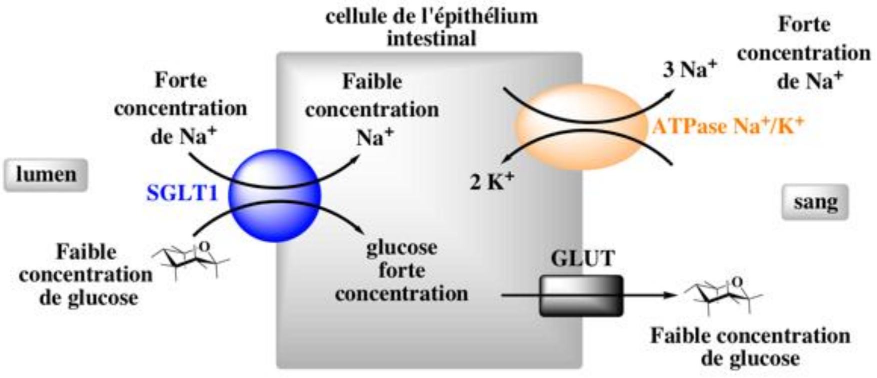


Figure 19. Sodium-calcium exchanger (Na^+/Ca^{2+})
(Klabunde, 2023)

➤ Symport

Symporters allow the simultaneous transport of two components in the same direction. One moves down its concentration gradient, while the other is transported against its gradient. A typical example is the Na^+/glucose cotransporter (SGLT): this transporter uses the sodium concentration gradient, which is maintained by the Na^+/K^+-ATPase pump, to enable the active uptake of glucose into cells (**Fig. 20**). Glucose and sodium move together in the same direction (symport).



E. Jaspard (2013)

Figure 20. Secondary active transport (Symport)

Conclusion

Mineral elements are essential for the growth and development of plants. Their transport, from the soil to the aerial organs, involves complex mechanisms of absorption, conduction, and membrane regulation. A better understanding of these processes helps to optimize agricultural practices, improve soil fertility, and ensure sustainable production while preserving ecosystems.

Chapter 3: Nitrogen Nutrition in Plants

Nitrogen is the fourth essential nutrient element for plants. It is a fundamental component of proteins, nucleic acids, hormones, chlorophyll, and many other primary and secondary compounds that are vital for plant growth and metabolism. Most plants absorb nitrogen from the soil in the form of nitrate (NO_3^-) or ammonium (NH_4^+). However, nitrogen availability is often limited, making it a key factor determining productivity in both natural ecosystems and agricultural systems.

I. Different Forms of Nitrogen in the Biosphere

The nitrogen cycle (**Fig. 21**) is a biogeochemical cycle that describes the transformation of the various forms of nitrogen: dinitrogen (N_2), nitrate (NO_3^-), nitrite (NO_2^-), ammonia (NH_3), and organic nitrogen (proteins, amino acids).

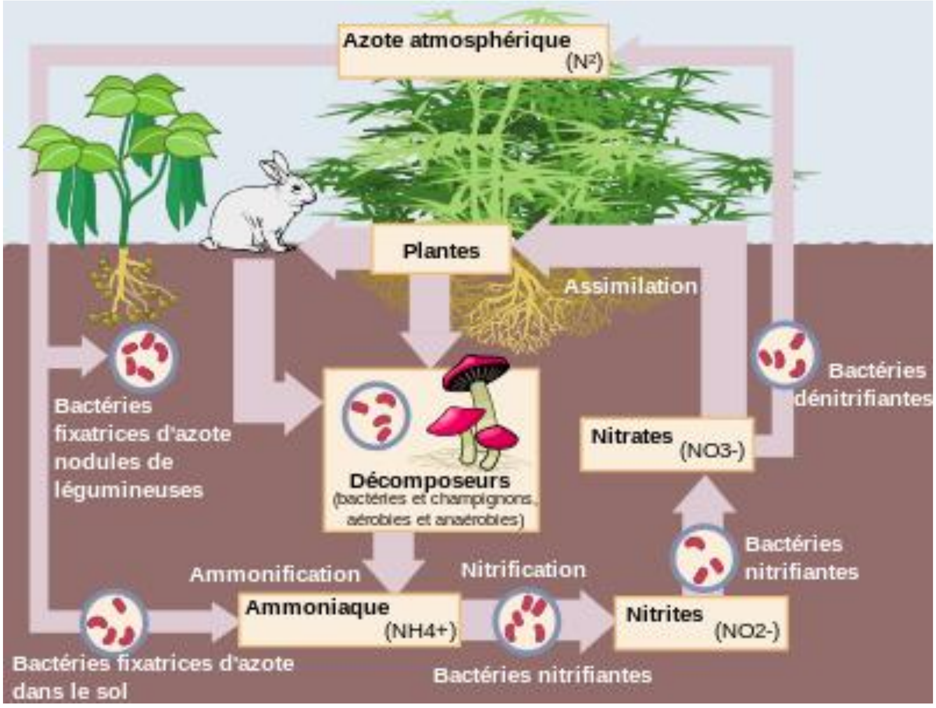


Figure 21. The nitrogen cycle (Dréo, 2006)

The atmosphere is the main reservoir of nitrogen in the form of molecular dinitrogen (N_2), which represents about 78% of the air by volume. However, in this form, nitrogen cannot be assimilated by most organisms. It must therefore be converted into a form usable by plants and, indirectly, by animals.

This process begins with the fixation of atmospheric nitrogen, carried out by:

- Free-living bacteria, such as *Azotobacter*.
- Symbiotic bacteria, such as *Rhizobium*, which live in association with the roots of legumes.

This fixation is made possible by a specific enzyme: nitrogenase.

Ammonia (NH_3) can also originate from the decomposition of organic matter, particularly dead organisms, through the action of saprophytic bacteria. It is then converted into nitrite (NO_2^-) and subsequently into nitrate (NO_3^-) by nitrifying bacteria during the nitrification process.

Plants mainly absorb nitrate ions (NO_3^-) and, to a lesser extent, ammonium ions (NH_4^+) present in the soil. These compounds are incorporated into amino acids and proteins, constituting the only source of assimilable nitrogen for animals.

In the soil, nitrogen exists in two main forms:

1. **Organic nitrogen**, stored in complex molecules (proteins, amino acids), mainly present in humus. Its decomposition by microorganisms releases nitrogen that can be used by plants.
2. **Mineral nitrogen**, in the form of nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+).

II. Origin of Soluble Nitrogen in the Soil

The mineral nitrogen present in the soil originates from the breakdown of organic nitrogen compounds through various microbial and physico-chemical processes. Several types of transformations can be distinguished:

- **Rapid transformation:** This involves an initial microbial degradation phase followed by a physico-chemical phase.
- **Slow transformation:** This concerns complex compounds such as cellulose and lignin, which are slowly oxidized and polymerized.
- **Mineralization:** This process includes three essential steps:
  - **Proteolysis:** Breakdown of proteins into peptides and amino acids.
  - **Ammonification:** Conversion of amino acids into ammonia (NH_3).
  - **Nitrification:** Conversion of ammonia into nitrites (NO_2^-), then into nitrates (NO_3^-).

III. Assimilation of Mineral Nitrogen by the Plant

Regardless of the ion absorbed by the plant, it is always converted into NH_4^+ before being assimilated. Nitrogen uptake and assimilation mainly occur:

- In the roots, where nitrates (NO_3^-) are converted into amides and ureides, which are transported via the xylem.
- In the stems and leaves, where nitrates are transformed into amides and then transported through the phloem.

III.1. Nitrate Assimilation

In nature, the main nitrogen source for plants is nitrate ions (NO_3^-). These are preferred over ammonium ions (NH_4^+) because they are less toxic to plant cells.

Once absorbed, nitrates are reduced to nitrites (NO_2^-), then to ammonia (NH_3), which is immediately metabolized.

- **Nitrate reductase**

The first reduction step is catalyzed by the enzyme nitrate reductase:

$$NO_3^- + H^+ + NADH \Longrightarrow NO_2^- + NAD^+ + H_2O$$

- **Nitrite reductase**

Nitrite is then reduced to ammonia:

$$NO_2^- + 7H^+ \Longrightarrow NH_3 + 2H_2O$$

III.2. Ammonium (NH_4^+) Assimilation

Ammonium can be assimilated via two main pathways:

- **Glutamate dehydrogenase (GDH)**

This enzyme is found in mitochondria and chloroplasts. It catalyzes the following reaction:

$$\alpha\text{-ketoglutarate} + NH_4^+ \Longrightarrow \text{Glutamate}$$

This is the process of reductive amination. The enzyme works with either NADPH or NADH, depending on the organelle involved.

- **Glutamine synthetase (GS) and glutamate synthase (GOGAT)**

These enzymes play a key role in ammonium fixation:

$$\text{Glutamate} + NH_4^+ \Longrightarrow \text{Glutamine}$$

$$\text{Glutamine} + \alpha\text{-ketoglutarate} \Longrightarrow 2\text{Glutamates}$$

This cycle allows the incorporation of ammonium into organic molecules, ensuring its assimilation without toxicity for the plant.

IV. Use of Atmospheric Nitrogen

Higher plants are not capable of directly fixing atmospheric nitrogen because they lack the necessary enzymatic machinery.

However, certain prokaryotic bacteria can fix nitrogen, either freely or in symbiotic association with plants.

IV.1. Free-Living Nitrogen Fixers

Free-living nitrogen-fixing bacteria are microorganisms capable of fixing atmospheric nitrogen (N_2) without living in symbiosis with a plant. These bacteria live autonomously in the soil (*Azotobacter*, *Clostridium*).

In addition to these bacteria, several genera of cyanobacteria (*Nostoc*) also fix nitrogen.

IV.2. Symbiotic Nitrogen Fixers

Some bacteria (the symbiont) establish a symbiotic relationship with plants (the host), providing them with nitrogen in exchange for carbon compounds and a favorable environment. Bacteria of the genus *Rhizobium* associate with legumes to form root nodules, where nitrogen fixation takes place.

IV.3. Infection Process

The symbiosis between rhizobia (*Rhizobium* bacteria) and legumes shows a high degree of host specificity.

These aerobic bacteria (*Rhizobium*) acquire the ability to fix atmospheric nitrogen only after penetrating the young roots of the host plants. This interaction triggers a plant response, visible through the formation of small swellings called nodules.

The process begins with the attraction of the bacteria to the rhizosphere (the area near the roots), guided by chemical compounds secreted by the plant. This phenomenon, called chemotaxis, involves molecules such as flavonoids.

These flavonoids activate the expression of Nod genes in the bacteria, inducing the synthesis of Nod factors. These factors are then recognized by specific receptors on the membrane of the plant's root cells.

In response to this molecular recognition, a series of cellular changes is initiated, one of the first being the curling of root hairs, which traps the bacteria.
An infection thread (or infection cord) then forms through remodeling of the cell wall, allowing the bacteria to penetrate the root tissues, particularly the cortical parenchyma (**Fig. 22**).

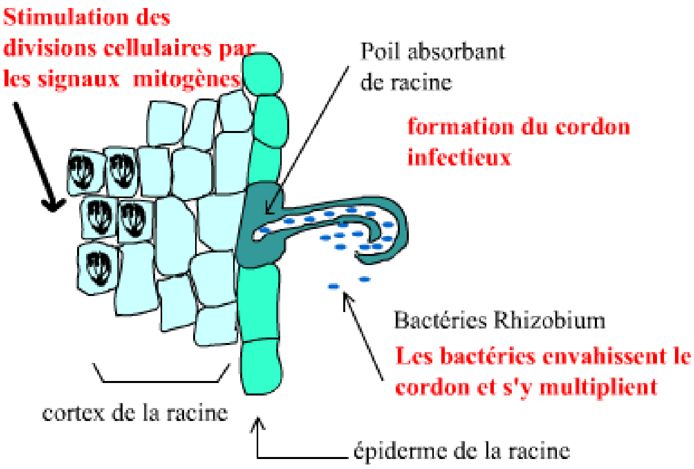


Figure 22. Infection process (Perrin, 2019)

The bacterial thread progresses through the cells of the root hair and then branches out within the cortical parenchyma. Once inside these cells, the threads rupture, releasing the *Rhizobium* bacteria, which then multiply actively. They undergo a morphological transformation: they increase in size and develop a characteristic Y-shaped form, typical of bacteroids.

The root nodule develops from the proliferation of the infected cells, forming an organized structure. At the same time, the root's vascular tissues produce branches that extend toward the developing nodule to ensure the supply of nutrients and the transport of the fixed nitrogen (**Fig. 23**).

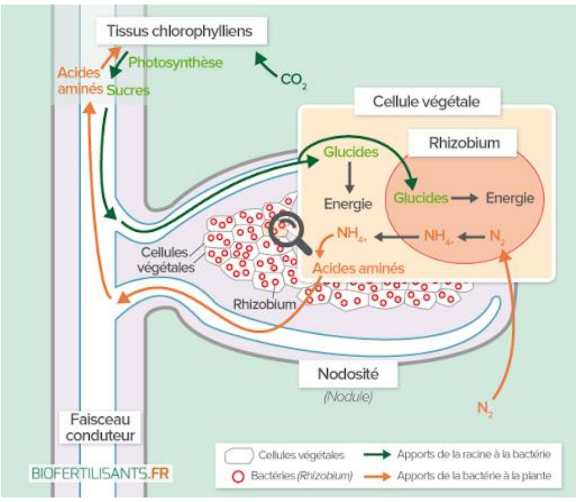


Figure 23. Root **nodule**
Source: biofertilisant.fr (http://www.ovh.com/fr)

In the roots, sugars and carbon compounds derived from photosynthesis flow and provide nutrients for the growth of the bacteria (indicated by green arrows). Simultaneously, the bacteria capture atmospheric dinitrogen (N_2) and convert it into ammonium (NH_4^+) (indicated by red arrows), which can then be assimilated by the plant.

IV.4. Nitrogen Fixation

Atmospheric nitrogen fixation by legume nodules is carried out by a key enzyme, nitrogenase, which is actually an enzyme complex composed of subunits and functions only under anaerobic conditions.

$$N_2 + 8H^+ + 8e^- + 16ATP \Longrightarrow 2NH_3 + H_2 + 16ADP + 16Pi$$

The activity of nitrogenase requires a constant supply of energy and a significant reducing power, which are provided by active respiration of the microsymbiont (**Fig. 24**).

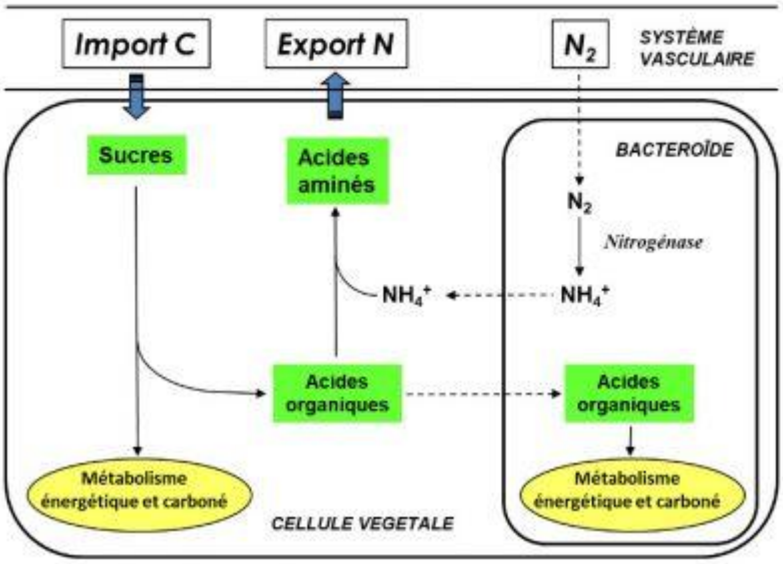


Figure 24. Carbon–nitrogen exchanges between the plant cell and the bacteria (*Encyclopédie de l'environnement)*

The plant's photosynthetic activity supplies oxidizable molecules for this metabolism and also provides carbon skeletons for the assimilation of the produced NH_4^+. There is therefore a close relationship between nitrogen fixation and photosynthesis, which can be one of the primary limiting factors for the efficiency of the symbiosis.

Conclusion

Nitrogen is an essential element for plants, but it must be converted into assimilable forms (nitrate and ammonium) through complex biological processes. The interaction between nitrogen-fixing bacteria and plants is a key factor in soil fertility and agricultural productivity.

Chapter 4: Carbon Nutrition (Photosynthesis)

I. Introduction to Photosynthesis

Photosynthesis is a fundamental bioenergetic process that enables plants, algae, and certain so-called photoautotrophic bacteria to convert the sun's light energy into chemical energy. This mechanism relies on the absorption of carbon dioxide and water to synthesize organic matter, mainly in the form of glucose, while releasing oxygen into the atmosphere.

Photosynthesis is arguably the most essential biochemical process in the living world. It plays a major role in maintaining the oxygen level in the atmosphere and is the primary source of organic matter and energy for most living organisms. It is thus the main pathway for converting inorganic carbon into organic carbon.

Plants, as well as certain bacteria and algae, are autotrophic organisms. They are primary producers because they form the first link in the food chain. In contrast, animals—including humans—are heterotrophic because they rely on preexisting organic matter for nourishment and survival.

II. Sites of Photosynthesis: The Chloroplasts

Photosynthesis occurs mainly in the leaves of chlorophyll-bearing plants, specifically in the palisade parenchyma cells located beneath the upper epidermis of the leaf (**Fig. 25**). It can also occur in the stem (though rarely).

The leaf is a flattened organ attached to the stem, whose morphology optimizes light exposure and gas exchange with the environment.

Each chlorophyll-containing cell has numerous chloroplasts (approximately 70 per cell). The chloroplast is an organelle essential for photosynthesis, as it contains the photosynthetic pigments, including chlorophyll. It has a biconvex shape and measures about 2 µm wide and 5 µm long.

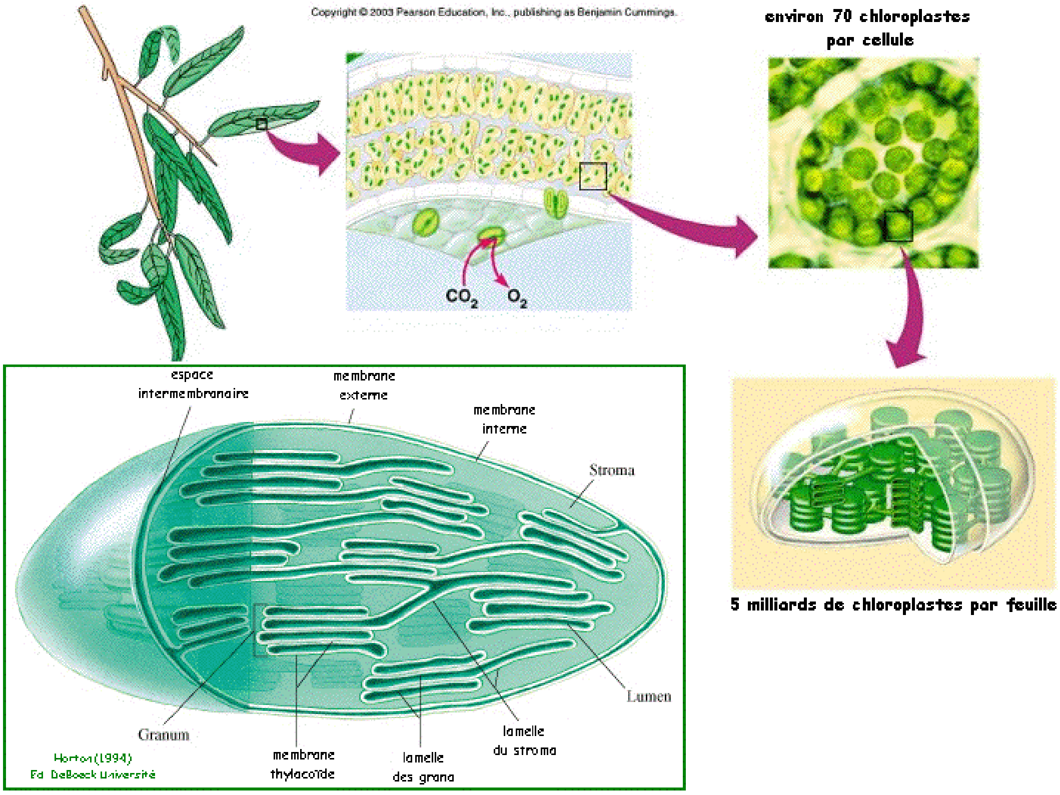


Figure 25. Location of photosynthesis (Horton et al., 1994)

The chloroplast is a semi-autonomous organelle of the plant cell. Like the mitochondrion, it has its own genetic material (**Fig. 26**) as well as a double phospholipid membrane:

- **The outer membrane** is composed, like any biological membrane, of phospholipids and proteins. It is relatively permeable.
- **The inner membrane** is less permeable and has folds called thylakoids.

These thylakoids can be:

•**Stacked**, forming *grana* (a *granum* = a stack of thylakoids).

•**Isolated**, forming *stromal thylakoids*, which extend into flattened tubes, ensuring continuity with the saccules of other grana.

The inner membrane encloses the internal region of the chloroplast, called the *stroma*. It contains unsaturated fatty acids, which maintain membrane fluidity, as well as photosynthetic pigments (chlorophylls and carotenoids), which are often associated with proteins

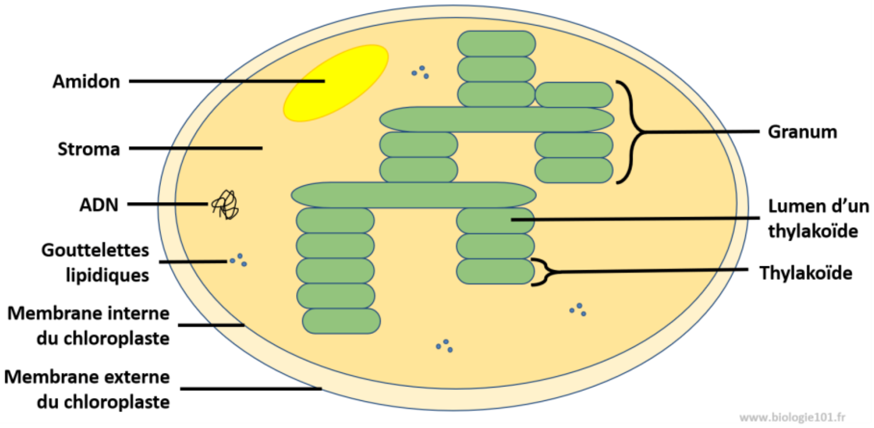


Figure 26. Structure of a chloroplast (www.biologie101.fr)

The chlorophylls are located within the thylakoid membranes, where they are arranged in parallel layers:

- Their hydrophilic poles (*porphyrin*) associate with supporting proteins.
- Their lipophilic poles (*phytol*) interact with the membrane lipids, positioned between carotenoids and other pigments.

  This highly organized structure plays a crucial role in the photochemical process, particularly by facilitating the transfer of excitation energy from pigment to pigment.

III. Photosynthetic pigments

Photosynthetic pigments play a vital role in capturing light energy in autotrophic organisms. They can be classified into three types: chlorophylls and carotenoids, which are present in all carbon-autotrophic plants, and phycobilins, which are found exclusively in algae and cyanobacteria.

III.1. Structure of photosynthetic pigments

III.1.1. Chlorophyll pigments

Chlorophyll pigments are chromoproteins, composed of a tetrapyrrolic core with a magnesium atom at its center (**Fig. 27**), and esterified with a very long C20 chain alcohol (phytol).

What is commonly referred to as *chlorophyll* is actually a mixture of several molecules with very similar chemical structures, combined within the grana. These include chlorophylls *a*, *b*, *c*, and *d*.

Chlorophylls *a* and *b* are the most abundant in higher plants and green algae, with proportions varying among species. Chlorophylls *c* and *d* are more commonly found in brown algae and cyanobacteria.

Chlorophylls *a* and *b* differ only by one chemical group (*methyl* –CH_3 in chlorophyll *a* and *aldehyde* –CHO in chlorophyll *b*).

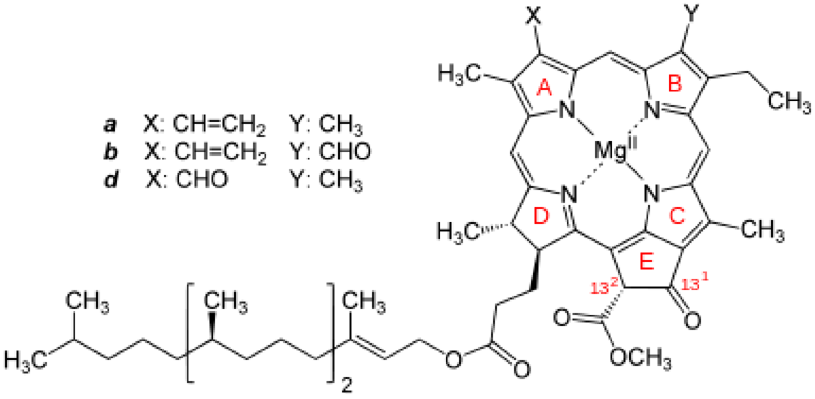


Figure 27. Structure of chlorophylls a, b, and d.
(Wikipedia)

Chlorophyll, being a pigment, has the characteristic of absorbing light in the visible spectrum, but the absorption peaks vary depending on the type of chlorophyll (**Fig. 28**).

- Chlorophyll a strongly absorbs at 430 nm (blue) and 660 nm (red).
- Chlorophyll b strongly absorbs at 445 nm (blue) and 645 nm (red).

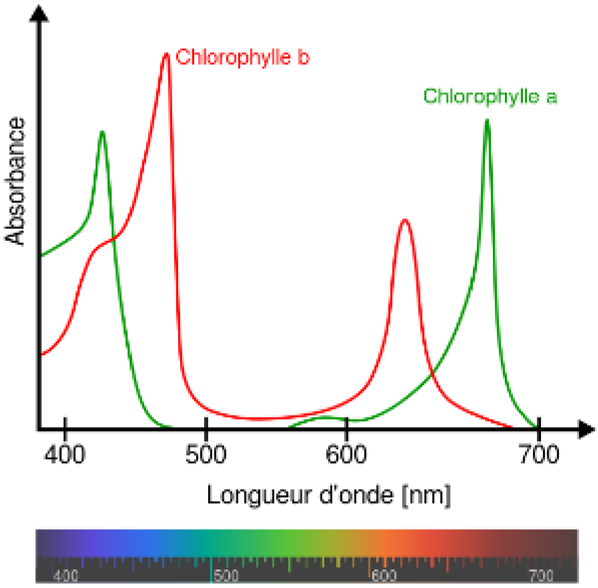


Figure 28. Absorption spectrum of chlorophylls a and b (Pugliesi, 2012)

Only chlorophyll a is active in photosynthesis. It is always associated with other pigments (accessory pigments), which capture photons at lower wavelengths and transfer the energy to chlorophyll a.

III.1.2. Carotenoids and Phycobilins

An accessory pigment is a non-chlorophyll pigment present in the chloroplasts of photosynthetic organisms. It plays a key role in absorbing wavelengths of light that chlorophyll does not efficiently capture.

a. Carotenoids

Carotenoids are lipophilic pigments, yellow or orange in color, and insoluble in water. They belong to the class of polyisoprenoid compounds, closely related to lipids.

They are molecules made up of 40 carbon atoms, with two cyclized ends connected by a long chain of eight isoprene units.

They include:

- **Carotenes**, which are tetraterpenes, C40 hydrocarbon compounds (**Fig. 29**), unsaturated, and precursors of vitamin A. They are found in all plants and phototrophic bacteria (β-carotene).

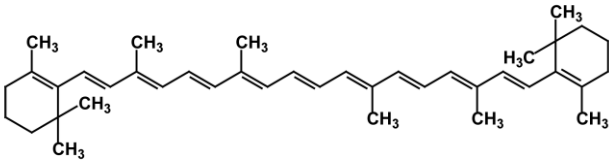


Figure 29. Molecular structure of β-carotene

- **Xanthophylls**, of the same type, have several alcohol or ketone functional groups (**Fig. 30**).

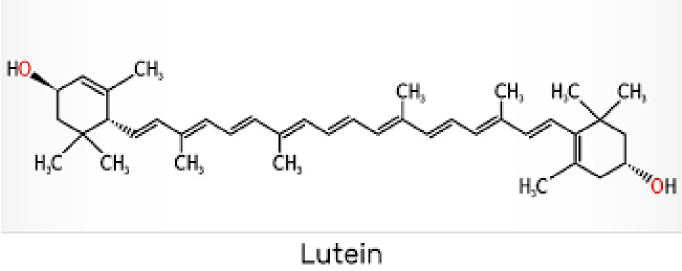


Figure 30. Molecular structure of lutein

The radiation absorbed by carotenes and xanthophylls is in the blue-green range (480 to 500 nm).

b. Phycobilins

Phycobilins are composed of an open tetrapyrrolic core associated with a protein. They are found within the photosystems of certain algae and photosynthetic bacteria such as cyanobacteria.

They include:

- **Phycoerythrins**: (red pigment) found in Rhodophyceae (red algae)
- **Phycocyanins**: (blue pigment) found in cyanobacteria

They absorb in the middle of the visible spectrum (green-yellow) and in the red.

The pigment composition of the cell determines the light-receiving characteristics of the organism and thus the absorption spectrum of light radiation (**Fig. 31**). The absorbed radiation is used for photosynthetic activity and defines the action spectrum.

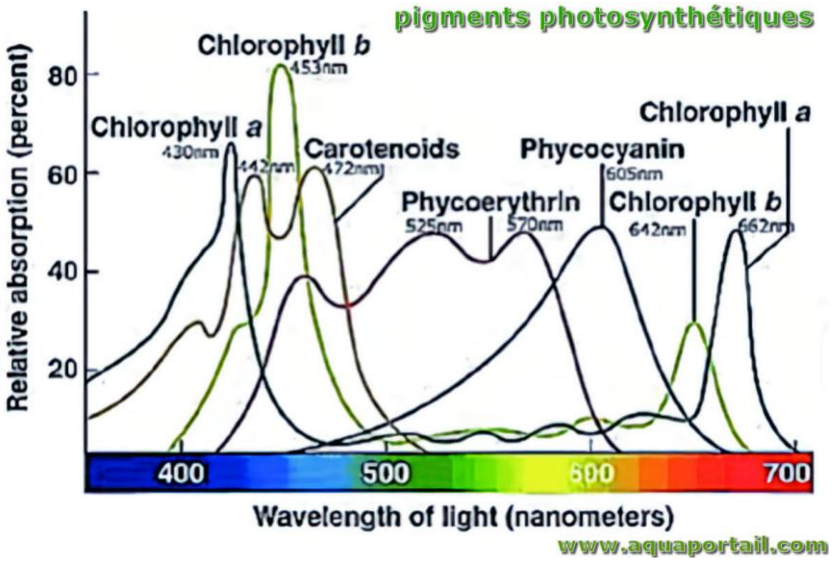


Figure 31. Absorption spectra of photosynthetic pigments

III.2. Role of Photosynthetic Pigments

The role of pigments during the light phase can be either active or accessory.

III.2.1. Active pigments and photosystems

Active pigments are directly involved in the photochemical process, converting light energy into chemical energy. This conversion relies on two specific chlorophyll a complexes:

- **P680**: This pigment forms the reaction center of Photosystem II (PSII).
- **P700**: This pigment forms the reaction center of Photosystem I (PSI).

III.2.2. Accessory pigments

Accessory pigments include other forms of chlorophyll a (called holochromes) as well as other pigments such as chlorophyll b, carotenoids, and phycobilins. They play a key role by transferring the absorbed energy to the active pigments through resonance.

III.2.3. Fate of absorbed energy

When an assimilating pigment absorbs radiation, it switches to an unstable excited electronic state.

The return to the ground state is accompanied by the release of the stored energy, either by:

- transferring its energy to a nearby molecule (by resonance), or
- losing an electron (photochemical conversion).

IV. Mechanisms of Photosynthesis

Photosynthesis occurs in two main phases: the light phase and the dark phase.

IV.1. The light phase (photochemical phase)

The light reactions take place in the thylakoids and involve two photosystems (PS II and PS I):

Light is captured in the form of photons, whose energy potential varies according to their wavelength. The absorption of this energy has two consequences: electron transport and proton release.

IV.1.1. Structure of Photosystems

Photosystems are the light-receiving centers located in the thylakoid membranes within the chloroplasts.

A photosystem (PS), or photosynthetic unit, is a complex formed by proteins and pigments. It includes a light-harvesting antenna and a reaction center.

Light-harvesting antenna: composed of specific proteins that have the ability to form stable bonds with photosynthetic pigments (**Fig. 32**).

It ensures the efficient capture of photons through photosynthetic pigments and transfers the excitation energy to the reaction center.

Reaction center: formed by a dimer of chlorophyll a (a trap molecule and a core molecule), along with several proteins that perform various functions (electron transfer, binding to electron carriers, etc.).

This assembly forms the core of the photosystem. Other protein molecules are also present, fulfilling additional roles such as interactions with other membrane components and regulatory functions.

When a pigment in the light-harvesting antenna captures a photon, it enters an excited state. This excitation is transferred from pigment to pigment until it reaches the reaction center, where it is converted into chemical energy.

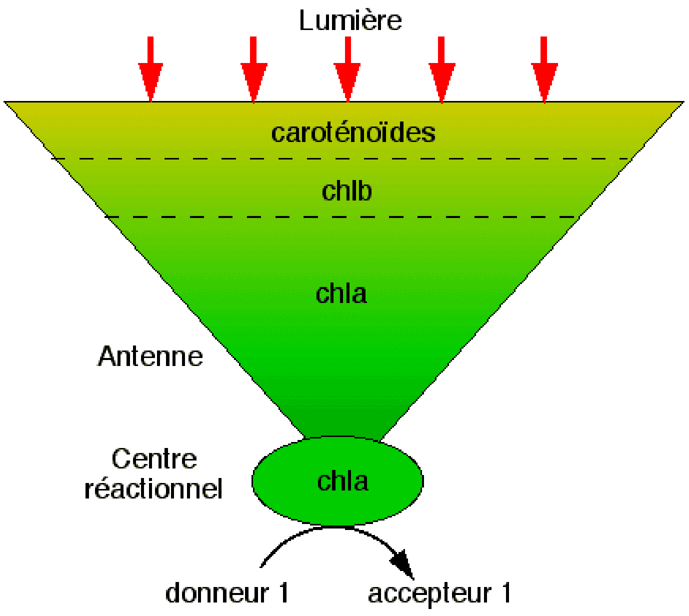


Figure 32. Schematic representation of a photosystem (Gantet et al, 2002)

IV.1.2. Mechanism of Photosystems

Two photosystems, called PS II and PS I, operate successively during the photochemical phase; their reaction centers correspond respectively to the holochromes P680 and P700 of chlorophyll *a*.

a. Photosystem II (PSII)

Photosystem II has as its reaction center a pair of chlorophyll *a* molecules called P680 (capable of absorbing light with a wavelength less than or equal to 680 nm).

The light energy is captured by the light-harvesting antenna, which then transfers it to the P680 complex.

The absorption of photons by a P680 chlorophyll molecule excites its electrons, giving them enough energy to be transferred to a primary electron acceptor, pheophytin (a chlorophyll molecule lacking magnesium).

These electrons are then transported along an electron transport chain, passing successively through a plastoquinone and the cytochrome b6f complex, where they induce the transfer of protons (H^+) from the stroma to the lumen (the intrathylakoid space). The accumulation of these protons generates an electrochemical gradient, which allows ATP synthase to convert ADP into ATP (**Fig. 33**).

$$\mathrm{ADP} + \mathrm{Pi} \longrightarrow \mathrm{ATP}$$

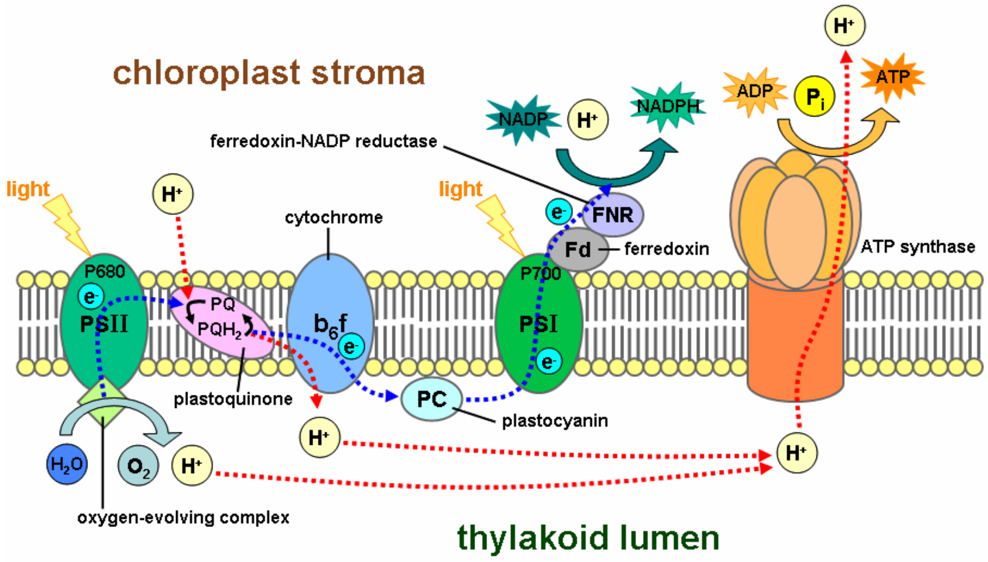


Figure 33. Diagram of a thylakoid membrane, showing the photosystems, ATP synthase, and the electron acceptor chain of non-cyclic photophosphorylation (Wikipedia).
PSII: Photosystem II; **PQH$_2$:** Plastoquinone; **cyt b$_6$f:** Cytochrome b$_6$f complex; **PC:** Plastocyanin;
PSI: Photosystem I; **Fd:** Ferredoxin; **FNR:** Ferredoxin–NADP$^+$ reductase

After passing through the cytochrome complex, the electrons are carried by a plastocyanin to Photosystem I (PSI).

The chlorophyll *a* of P680, having lost electrons, must regain them to continue functioning; these are supplied by the photolysis of water.

b. Photosystem I (PSI)

Photosystem I consists of a pair of chlorophyll *a* molecules, called P700 (which absorbs light with a wavelength less than or equal to 700 nm).

To continue photosynthesis, additional light energy is needed, which is absorbed by the light-harvesting antenna and transferred to the P700 complex. This complex then releases new electrons, which are captured by the primary acceptor (chlorophyll A_0).

These electrons are passed to a ferredoxin, which transfers them to a ferredoxin–$NADP^+$ reductase to reduce a molecule of $NADP^+$ to NADPH + H^+ (**Fig. 33**).

$$NADP^+ + 2e- + 2H \longrightarrow NADPH + H^+$$

The chlorophyll *a* of P700 has therefore lost electrons, which it must regain for the system to function; these electrons are supplied by PSII.

IV.1.3. Electron Transport in the Light Phase

The light-dependent reactions can follow two pathways: non-cyclic electron transport and cyclic electron transport.

IV.1.3.1. Photolysis of Water and Non-Cyclic Electron Transport (Non-Cyclic Photophosphorylation)

In Photosystem II (PSII), photolysis of water occurs, which is a crucial step in photosynthesis. When it absorbs light energy, PSII undergoes photo-oxidation, resulting in the loss of electrons.

To restore its balance and continue functioning, it receives new electrons from the water molecule, which thus acts as the primary electron donor. Under the effect of light energy, the water molecule undergoes an oxidation reaction, leading to the release of:

- Electrons, which are captured by PSII and then transferred along the electron transport chain.
- Protons (H^+), which accumulate in the intrathylakoid space, contributing to the formation of a proton gradient necessary for ATP synthesis.
- Oxygen (O_2), which is released into the atmosphere as a by-product of the reaction.

The chemical equation for the photolysis of water is

$$\mathbf{H_2O \longrightarrow 2\ H^+ + ½ + 2\ e^-}$$

This process is at the heart of non-cyclic photophosphorylation, which results in the production of ATP and NADPH, molecules essential for the dark phase of photosynthesis.

The overall equation for non-cyclic photophosphorylation in green plants is:

$$\mathbf{2\ H_2O + 2\ NADP^+ + 3\ ADP + 3\ Pi + lumière \longrightarrow 2\ NADPH + 2\ H^+ + 3\ ATP + O_2}$$

IV.1.3.2. Cyclic Electron Transport (Cyclic Photophosphorylation)

In this pathway, only Photosystem I (PSI) is involved.

The electrons excited by light in PSI, instead of being transferred to NADP⁺ reductase via ferredoxin, follow an alternative route:

1. Ferredoxin transfers the electrons to plastoquinone (PQ) via a cytochrome.
2. The electrons then travel through the electron transport chain, creating a proton flow into the intrathylakoid space.
3. These electrons finally return to PSI, filling the vacancies they initially created there (**Fig. 34**).

Unlike non-cyclic transport, this cyclic route does not produce NADPH but promotes ATP production by generating a proton gradient.

This mechanism is essential under certain conditions, especially when the plant has an increased need for ATP to balance the energy demands of the dark phase of photosynthesis

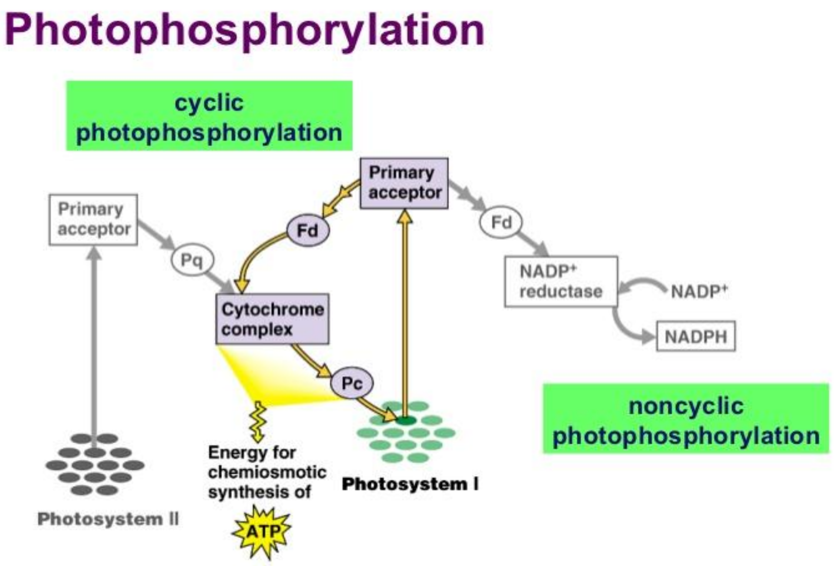


Figure 34. Cyclic and non-cyclic photophosphorylation
https://www.toppr.com

IV.2. Dark phase (biochemical phase)

The dark phase of photosynthesis, also known as the Calvin-Benson cycle or biosynthetic phase (**Fig. 35**), is a metabolic process that takes place in the stroma of chloroplasts. It involves the assimilation of carbon dioxide (CO_2) using the energy supplied by ATP and the reducing power of NADPH, both produced during the photochemical phase.

This stage is essential for carbon fixation and the synthesis of organic compounds required for plant growth and metabolism.

The Calvin cycle occurs in three main phases, followed by a fourth step leading to sugar synthesis:

- CO_2 fixation (carboxylation)
- Reduction of the fixed carbon
- Regeneration of the CO_2 acceptor
- Sugar synthesis

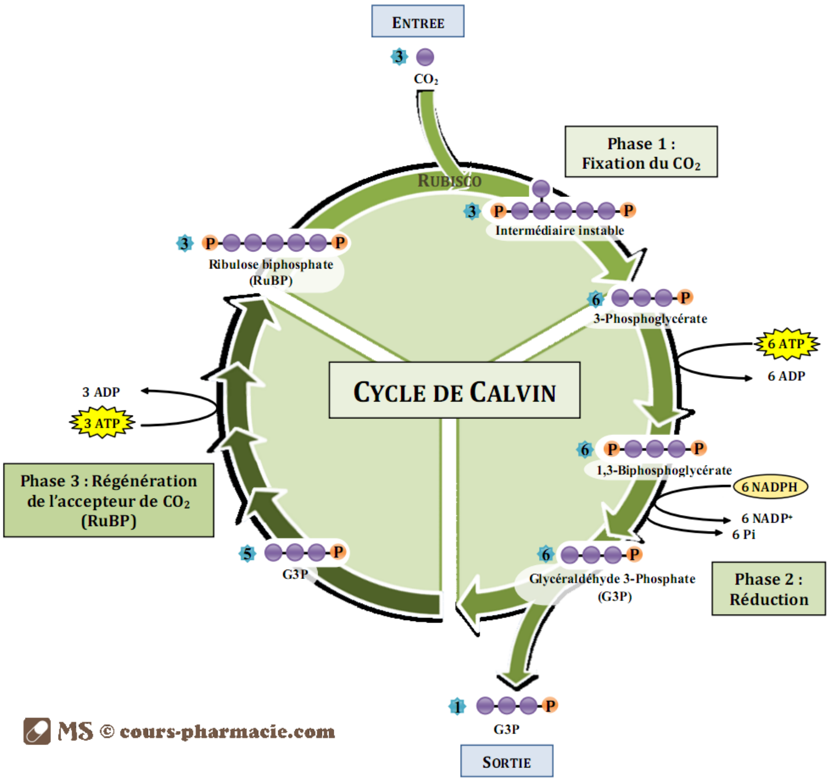


Figure 35. Diagrams representing the Calvin cycle.

1. CO_2 Fixation

This step consists of incorporating atmospheric CO_2 into an organic molecule, which is ribulose-1,5-bisphosphate (RuBP) (a five-carbon compound).This reaction is catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and results in the production of two molecules of 3-phosphoglycerate (3-PGA) (each containing three carbon atoms).

The carboxylation can be written in simplified form as follows:

3 D-Ribulose-1,5-bisphosphate + CO_2 + H_2O ⟶ 6 3-Phospho-D-glycerate

$3\ C_5H_8P_2O_{11} + 3\ CO_2 + 3\ H_2O \longrightarrow 6\ C_3H_3PO_7$

2. Reduction of Fixed Carbon

The second phase of the Calvin cycle corresponds to the reduction of 3-phosphoglycerate. First, it is phosphorylated by ATP to produce 1,3-bisphosphoglycerate, which is then reduced by NADPH to form glyceraldehyde-3-phosphate (G3P), a simple sugar.

3-phosphoglycerate + ATP ⟶ 1,3-bisphosphoglycerate + ADP

$6\ C_3H_3PO_7 + 6\ ATP \longrightarrow 6\ C_3H_3P_2O_{10} + 6\ ADP$

1,3-bisphosphoglycerate + NADPH + H^+ ⟶ glyceraldehyde-3-phosphate + $NADP^+$ + Pi

$6\ C_3H_3P_2O_{10} + 6\ NADPH \longrightarrow 6\ C_3H_5PO_6 + 6\ NADP^+ + 6\ Pi$

3. Regeneration of the CO_2 Acceptor (RuBP)

The glyceraldehyde-3-phosphate (G3P) formed can follow different pathways: one-sixth of it will be used by the cell as a carbohydrate component, while the remaining five-sixths will be used to continue the Calvin cycle. The regeneration of RuBP, which will be reused to fix CO_2, occurs in several steps and requires ATP.

5 Glyceraldehyde-3-phosphate ⟶ 3 ribulose-5-phosphate + 2 Pi

$5\ C_3H_5PO_6 \longrightarrow 3\ C_5H_8PO_7 + 2\ Pi + OH^-$

3 ribulose-5-phosphate + 3 ATP ⟶ 3 ribulose-1,5-bisphosphate + 3 ADP

$3\ C_5H_8PO_7 + 3\ ATP \longrightarrow 3\ C_5H_8P_2O_{11} + 3\ ADP$

4. Sugar Synthesis

Two molecules of G3P, out of the twelve produced during the Calvin cycle, will enter the plant’s metabolic pathways, where they are mainly converted into carbohydrates:

- Either in the form of sucrose (α-Glu-Fructose), which is the transport form in the phloem sap

  2 Glyceraldehyde-3-phosphate ⟶ glucose-6-phosphate

  $2\ C_3H_5PO_6 + 2\ [H] \longrightarrow C_6H_{13}O_9P + Pi + 3\ O_2$

- Or in the form of starch, which is the storage form (α-1,4-Glu)

IV.3. Photosynthesis Balance

During photosynthesis, each CO_2 molecule fixed in the Calvin cycle requires 3 ATP and 2 NADPH.

However, the basic carbohydrates used in energy metabolism are hexoses. To synthesize one hexose molecule ($C_6H_{12}O_6$), 6 CO_2 molecules must be fixed, which requires 6 turns of the Calvin cycle. This leads to the consumption of 18 ATP and 12 NADPH (**Fig. 36**).

The overall equation for photosynthesis can therefore be written as follows:

$$6\,CO_2 + 18\,ATP + 12\,NADPH + 12\,H_2O \longrightarrow C_6H_{12}O_6 + 18\,ADP + 18\,Pi + 12\,NADP^+$$

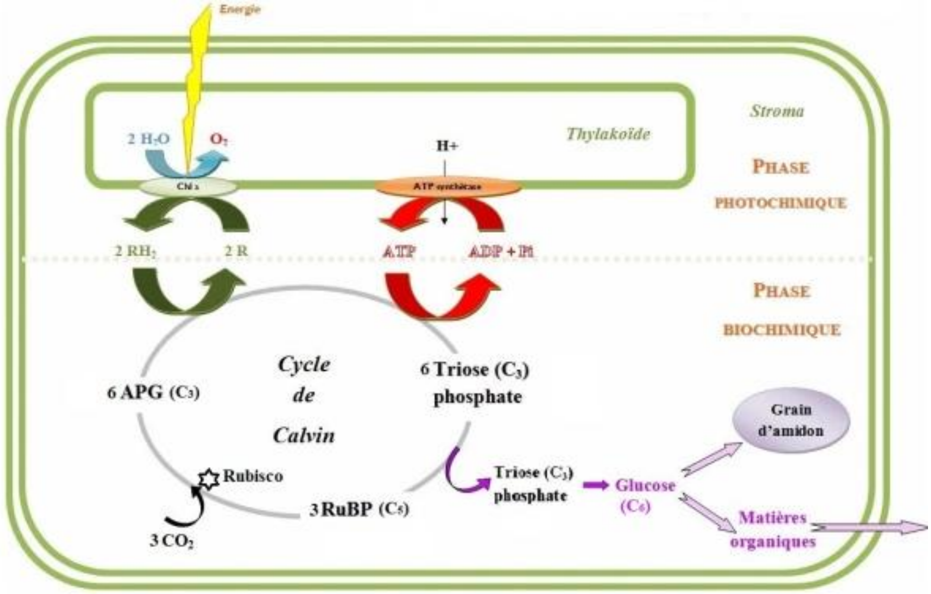


Figure 36. Overview of photosynthesis at the chloroplast level (svt.ac-dijon.fr)

V. The Different Types of Photosynthesis: C_3, C_4, and CAM Plants

There are different modes of CO_2 fixation in plants during photosynthesis. These mechanisms vary in the efficiency of the carboxylation step.

The type of photosynthesis a plant uses is determined by the number of carbon atoms in the first organic molecule formed during CO_2 fixation.

V.1. C_3 Plants

The majority of plants are classified as C_3 plants, as they use three-carbon molecules (3-phosphoglycerate) for sugar formation. They mainly grow in temperate environments (e.g., cereal crops, spinach, tomato, apple tree, peach tree).

V.2. C_4 and CAM Plants

Stomata play an important role in regulating the plant's transpiration, which often takes priority over photosynthetic efficiency. In other words, the opening and closing of stomata will always aim to conserve the plant's water, even if it happens at the expense of photosynthesis.

Some plants living in more challenging environments than C_3 plants have developed alternative strategies to maintain some photosynthetic activity despite these limitations. This is the case for C_4 and CAM plants.

C_4 plants also live in temperate regions but under specific conditions, such as saline soils. CAM plants inhabit arid environments and are typically succulent species.

V.2.1. C_4 Plants

C_4 plants have the special ability to enhance CO_2 assimilation through an additional reaction that occurs in the cytoplasm. They still use three-carbon molecules but also produce four-carbon molecules that act as a temporary CO_2 reservoir.

In this additional reaction, CO_2 binds to phosphoenolpyruvate (PEP, a three-carbon molecule) to form a four-carbon compound, oxaloacetate, which is then reduced to malate by NADPH. Malate subsequently releases pyruvate and CO_2, which is then reused in the Calvin cycle.

In this pathway, CO_2 forms a four-carbon acid (oxaloacetate), and two types of cells are involved (**Fig. 37**):

- **Mesophyll cells** (the tissue layer between veins, the site of the Calvin cycle in C_3 plants; they lack Rubisco) where the carboxylation step occurs.
- **Bundle sheath cells** (which contain Rubisco) where the decarboxylation step takes place.

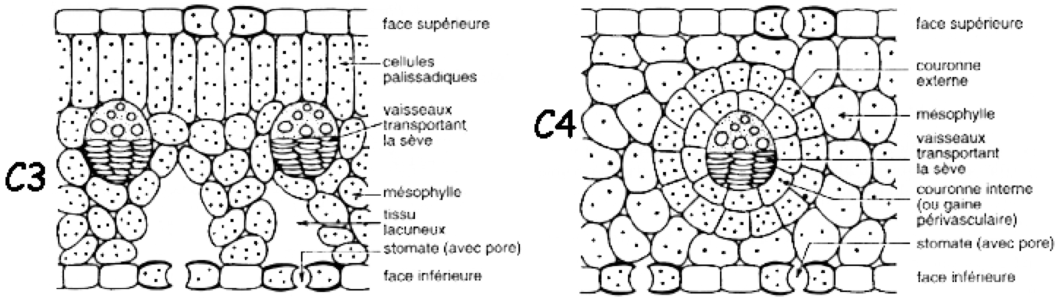


Figure 37. Anatomy of C_3 plants and C_4 plants (known as Kranz anatomy)
(Laval-Martin & Mazliak, 1995)

Plants with this mechanism possess another enzyme capable of fixing CO_2: phosphoenolpyruvate carboxylase, or PEPcase (which lacks oxygenase activity). This enzyme is present exclusively in the mesophyll cells.

The mechanism of carbon dioxide fixation in C_4 plants (**Fig. 38**) is as follows:

Atmospheric CO_2 is first hydrated to bicarbonate (HCO_3^-).

Phosphoenolpyruvate (PEP) and HCO_3^- combine through a carboxylation reaction catalyzed by PEPcase, forming oxaloacetate (a four-carbon acid).

Depending on the C_4 plant species, oxaloacetate is either reduced to malate or transaminated to aspartate. These C_4 acids then move into the neighboring bundle sheath cells through intercellular “channels” called plasmodesmata.

The walls of bundle sheath cells are impermeable to gases. As a result, the decarboxylation of the C_4 acids significantly increases the local CO_2 concentration. This CO_2 enrichment makes photorespiration virtually zero or very low in C_4 plants, especially since the mesophyll cells lack Rubisco.

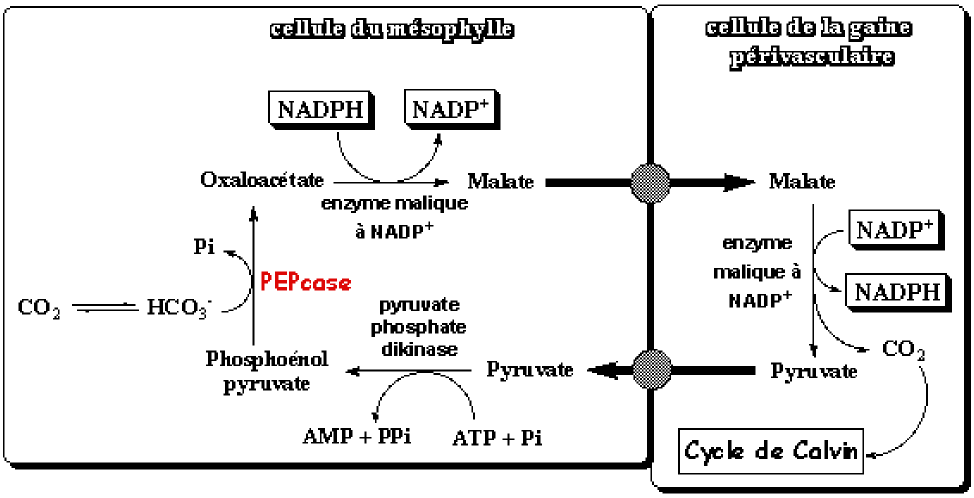


Figure 38. Photosynthesis and carbon dioxide fixation in C_4 plants (Simon, 2009)

V.2.2. CAM Plants (Crassulacean Acid Metabolism)

CAM plants (Crassulacean Acid Metabolism) are species that live in arid environments (examples of CAM plants include pineapple and agave). They require efficient water conservation and therefore have a finely regulated transpiration process. They use exactly the same additional reaction as C_4 plants but differ in that they assimilate CO_2 at night. This is made possible by the characteristic ability of CAM plants to open their stomata during the night.

The CO_2 is thus stored in the form of malate, which will be used during the day when the light phase takes place (**Fig. 39**).

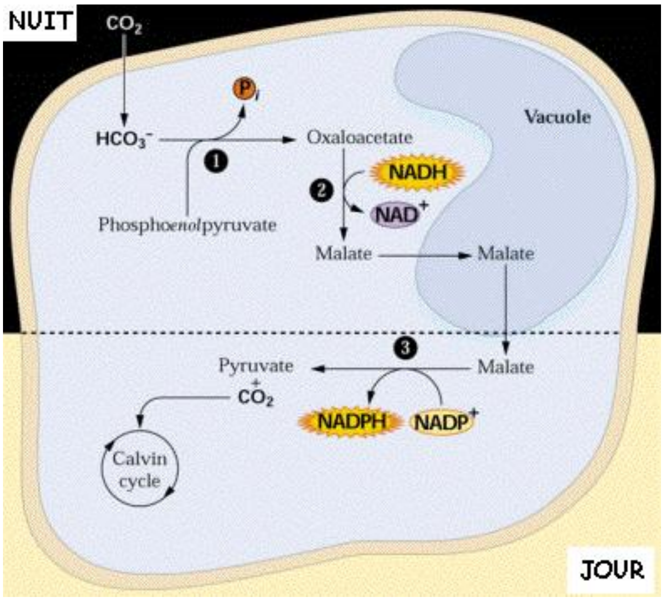


Figure 39. Photosynthesis in CAM plants (Simon, 2009)

Like C_4 plants, succulent plants (desert species, plants in saline environments) possess both Rubisco and PEPcase. Their mode of functioning allows them to minimize water loss. However, in CAM plants, CO_2 fixation is not separated spatially (mesophyll / bundle sheath) but temporally: night/day.

During the night :

- Stomata are open
- PEPcase forms oxaloacetate
- Malate is stored in the vacuole of the photosynthetic cells

During the day :

- Stomata are closed
- Malate is decarboxylated
- The Calvin cycle takes place
- The pyruvate produced from malate decarboxylation is converted into starch through gluconeogenesis and stored in the chloroplast.

VI. The Role of Environmental Factors in Photosynthesis

The rate of photosynthesis can be influenced by various environmental factors, such as light (the energy source), carbon dioxide (CO_2, the carbon source), temperature (which affects all biochemical reactions), and water (a source of electrons).

VI.1. Light

Light is the main external factor influencing photosynthesis. It affects photosynthesis through its intensity, quality (color), and duration of exposure.

- ✓ **Light Intensity**

A minimum level of illumination is essential for photosynthetic activity to be beneficial and to cover the plant's basic needs, especially to compensate for respiration. The effect of light intensity varies with plant type: shade-loving plants (sciophytes) require low light levels, while sun-loving plants (heliophytes) need higher light levels.

- ✓ **Light Quality**

The light within the range of photosynthetically active radiation spans from 400 to 700 nm (the spectrum of white light). However, blue and red light are more effective for photosynthesis than green light, because chlorophyll absorbs these specific wavelengths more efficiently (Fig. 28).

- ✓ **Duration of Light Exposure**

The duration of light exposure also affects photosynthesis. The longer a plant is exposed to light, the more energy it accumulates for biochemical processes, enhancing photosynthetic efficiency. Conversely, too short an exposure limits the energy available for carbohydrate synthesis.

VI.2. Carbon Dioxide (CO_2)

Carbon dioxide is one of the essential reactants in photosynthesis. It is absorbed through the leaf stomata and used in the Calvin cycle for carbohydrate production. The atmospheric concentration of CO_2 is about 0.035%, which can limit the rate of photosynthesis under moderate light conditions. Increasing the CO_2 concentration in the air can thus enhance photosynthesis. The optimal CO_2 concentration to maximize photosynthesis is around 0.1%. However, beyond this point, other factors such as light intensity and temperature become limiting.

VI.3. Temperature

Temperature directly affects the activity of the enzymes involved in photosynthesis, especially Rubisco. At low temperatures, enzyme activity decreases, which reduces the photosynthesis rate. As temperature rises, enzyme efficiency improves up to a critical threshold, generally between 35 °C and 40 °C, beyond which enzymes may denature and photosynthesis may slow down or stop.

Additionally, excessive heat causes stomata to close to reduce water loss, thereby limiting CO_2 intake.

For most plants, the optimal temperature for effective photosynthesis is between 20 °C and 30 °C, although this range can vary depending on species and environmental conditions.

VI.4. Water

Water is used during photolysis to release oxygen and produce the electrons needed for photosynthesis reactions.

Water stress therefore leads to a significant decrease in the photosynthesis rate.

Chapter 5: Photorespiration

Introduction

Photorespiration is the set of reactions carried out by photosynthetic organisms as a result of the oxygenase activity of Rubisco.

Indeed, Rubisco is an enzyme with two activities (**Fig. 40**):

- **Carboxylase**: it fixes CO_2 onto ribulose-1,5-bisphosphate (RuBP), initiating the Calvin cycle and enabling the production of sugars (Rubisco's affinity for CO_2 is higher than for oxygen).
- **Oxygenase**: it can also fix O_2 onto RuBP, generating an undesirable product: phosphoglycolate.

Respiration is a light-independent process — called "dark respiration" — and is responsible for CO_2 release.

The emission of CO_2 increases when the plant is exposed to light. The cause of this additional emission comes from another type of respiration that occurs only in the light and whose intensity depends on the plant's photosynthetic activity. This is **photorespiration**.

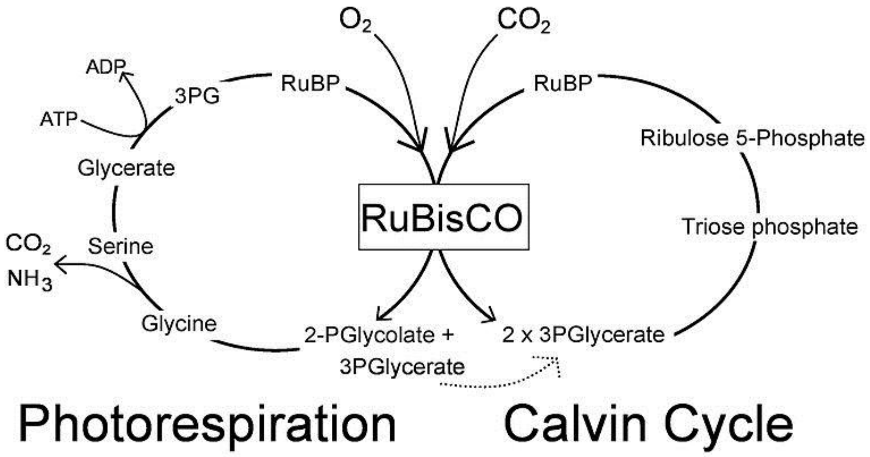


Figure 40. Simplified diagram of Photorespiration
(Purdon, 2013)

Unlike photosynthesis, photorespiration:

- ✓ Consumes energy (ATP, NADH)
- ✓ Releases CO_2, reducing the efficiency of carbon fixation

It is therefore seen as a metabolic waste, however, it is unavoidable and also plays a protective role against the accumulation of toxic intermediates and photo-oxidative stress.

The oxygenase activity of Rubisco is stimulated under certain conditions:

High temperatures: increase the solubility of O_2 relative to CO_2.
Drought: stomata close to limit water loss, which lowers the internal CO_2 concentration.

1. Mechanism

Photorespiration takes place in three cellular organelles: the chloroplast, the peroxisome, and the mitochondrion (**Fig. 41**).

Chloroplast: site of phosphoglycolate formation.

When Rubisco fixes O_2, RuBP is split into two molecules;

- **One molecule of 3-phosphoglycerate (3-PGA)**, which can be used in the Calvin cycle.
- **One molecule of 2-phosphoglycolate**, a toxic metabolite for the cell that must be rapidly recycled.
- **Phosphoglycolate** is dephosphorylated to glycolate.

Peroxisome:

- **Glycolate** is transported to the peroxisome, where it is converted into glyoxylate and then into glycine.

Mitochondrion:

- **Glycine** enters the mitochondrion, where two glycine molecules produce one serine molecule, one CO_2, and one NH_3.
- **Serine** returns to the peroxisome, is transformed into hydroxypyruvate, and then into 3-PGA in the chloroplast, thus re-entering the Calvin cycle.

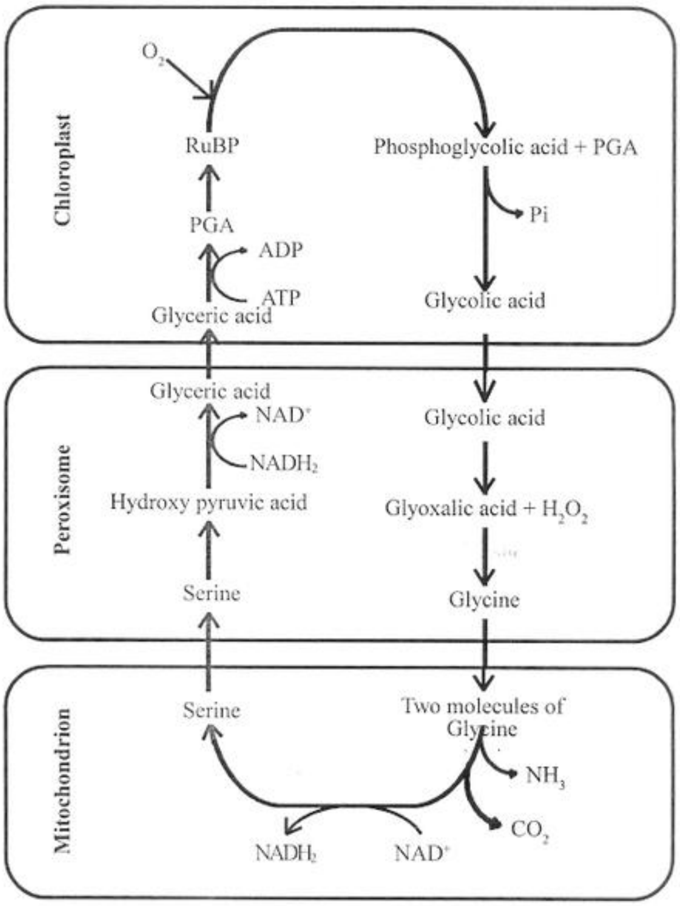


Figure 41. General scheme of photorespiration.
(Santhosh, 2014)

2. Impact on Plant Growth

Photorespiration reduces photosynthetic yield, especially in so-called C_3 plants (wheat, rice, soybean) that lack specific mechanisms to concentrate CO_2 around Rubisco.

Some plant species have developed mechanisms to limit photorespiration:

- **C_4 plants** (maize, sugarcane): they fix CO_2 in specialized cells (mesophyll, then bundle sheath cells), creating a high CO_2 concentration around Rubisco and thus limiting its oxygenase activity.
- **CAM plants** (cacti, pineapple): they fix CO_2 at night, store it as organic acids, and release it during the day for photosynthesis, thereby reducing water loss and photorespiration.

Conclusion

Mitochondrial respiration results in a loss of 40% to 50% of the daily photosynthetic output at the whole-plant level.

Photorespiration accounts for a loss of 30% of the total assimilated CO_2.

At the end of a 24-hour day, only 20% to 30% of the assimilated carbon remains in the plant.

Photorespiration is a paradoxical metabolism: although it is detrimental to the photosynthetic activity of plant cells, it appears to be useful, or even necessary, for other cellular functions. Indeed, some studies have suggested that photorespiration may be essential for the fixation of nitrogen from soil nitrates.

Despite reducing the efficiency of photosynthesis, it helps protect the plant by preventing the accumulation of toxic compounds.

Understanding and managing photorespiration is a strategic lever to address the challenges of agricultural production in the context of climate change and represents a major goal for:

- Improving crop yields by limiting carbon and energy losses.
- Selecting or genetically modifying plants to perform better under climate stress conditions (drought, heat).
- Exploring new metabolic pathways inspired by bacteria or algae to bypass photorespiration.

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