4. Mineral Nutrition

The absorption of water necessarily leads to the absorption of mineral elements because water in the soil is loaded with nutrients (minerals). The mineral nutrition of a plant involves the mechanisms that, after absorption, ensure the transport, storage, and utilization of the mineral ions necessary for the plant's metabolism and growth. These mechanisms take place in various organs of the vegetative system (roots, stems, and leaves).

Plants take up mineral salts that exist in the soil in the form of ions and penetrate through the roots. Large root surfaces and active absorption systems explain why, despite the low concentrations of ions in the soil solution, the acquisition of mineral nutrients by plants is a highly efficient process. Chlorophyll-containing plants extract essential mineral substances from their surroundings (soil, water, and air). The absence or deficiency of these substances disrupts their development.

Essential Elements (Macronutrients and Micronutrients)

An element is considered essential if, in its absence, the plant cannot complete its full development cycle, from seed to seed. It is irreplaceable by another element and directly contributes to the plant's metabolic reactions.

Macronutrients (besides C, H, and O):

N (Nitrogen), K (Potassium), Ca (Calcium), Mg (Magnesium), P (Phosphorus), and S (Sulfur) are considered macronutrients. In certain species, Si (Silicon) is also essential. Each of these elements represents at least 0.1% (0.1% to 4%) of the dry weight of the plant.

Nitrogen (N) is absorbed by the roots in the form of nitrate (NO_3^-) or ammonium (NH_4^+) ions, or, in some species, through nitrogen fixation by symbiotic bacteria.

Potassium (K), Calcium (Ca), Magnesium (Mg), Phosphorus (P), and Sulfur (S) are absorbed as ions: K^+, Ca^{2+}, Mg^{2+}, phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}), respectively.

Micronutrients (Trace Elements):

Micronutrients play an important role in the plant's health and growth. These include Boron (B), Manganese (Mn), Zinc (Zn), Chlorine (Cl), Molybdenum (Mo), Cobalt (Co), and Copper (Cu). They are absorbed in the following forms: Cl^-, Fe^{2+} or Fe^{3+} (depending on the species), Mn^{2+}, Zn^{2+}, borate ($H_2BO_3^-$), Cu^{2+}, Ni^{2+}, and MoO_4^{2-}.

The amounts of micronutrients assimilated by plants are in trace quantities, but their role in overall plant nutrition is crucial. They are present in the plant in very small amounts, usually not exceeding 0.01% of the dry weight.

Non-Essential Elements

Non-essential elements (optional) are divided into two categories:

Useful Elements: These are essential for some plants only, such as Na (Sodium), Si (Silicon), Co (Cobalt), Al (Aluminum), Se (Selenium), and Ti (Titanium).

Toxic Elements: These inhibit the growth and development of plants. Their action is often related to the blocking of an enzymatic system. When a mineral element is added in high concentrations, it becomes toxic, impairing the plant's growth and development.

Nitrogen (N)

Nitrogen is an essential nutrient for the growth and development of plants. It is a key component of amino acids, proteins, and several vitamins. A nitrogen deficiency leads to a marked reduction in chlorophyll (chlorosis), causing the yellowing of leaves, followed by a slowdown and halt in photosynthesis. This highlights the importance of nitrogen in plant nutrition.

Phosphorus (P)

Phosphorus is involved in energy transfer processes, including the storage and transport of energy in cells (ATP), the transmission of genetic information (nucleic acids), photosynthesis, and carbohydrate breakdown. Phosphorus is a key component of phosphorylated proteins (e.g., nucleoproteins, phosphoproteins). Moreover, many metabolic reactions require prior phosphorylation to occur. Phosphorus is essential for flowering, early development, fruit enlargement, and seed maturation.

Phosphorus Deficiency:

Plants deficient in phosphorus exhibit slowed growth.

Root development and population density are reduced.

Flowering and maturation are delayed.

Phosphorus deficiency leads to a decrease in protein and vitamin production.

Cold resistance is weakened.

Potassium (K)

Potassium acts as an activator for various enzymes. It increases cell pressure, regulates water use in plants, and reduces evaporation, thereby enhancing drought resistance. Potassium is the primary ion in cytoplasmic solutions and plays a fundamental role in both passive and active transmembrane exchanges within cells. It also improves chlorophyll assimilation and frost resistance.

Plants with high potassium needs include legumes, potatoes, beets, corn, and oats.

Potassium Deficiency:

Reduced flavor in fruits and vegetables.

Decreased resistance to frost and drought.

Increased transpiration and respiration.

Poorer storage quality for fruits and vegetables.

Magnesium (Mg)

Magnesium is a constituent of chlorophyll. It is involved in the formation of essential organic compounds like pectin and also acts as an enzyme activator.

Magnesium supports the absorption and transport of phosphorus to seeds, where it promotes lipid synthesis.

Magnesium helps prevent the excessive absorption of potassium by plants.

Calcium (Ca)

Calcium content in plants is usually similar to that of potassium, but its mobility and distribution in plant tissues differ significantly. Calcium strongly associates with carboxyl groups (COOH) in hemicelluloses and pectic compounds (carbohydrates in the plant cell wall that provide structural stability and flexibility). In the vacuole, calcium helps neutralize the electrical charge of anions (e.g., sulfates, phosphates). It also plays an essential role as a secondary biochemical messenger in the functioning of plant cellular machinery.

Micronutrients:

Micronutrients, which are part of certain protein structures, are particularly involved in redox reactions, which facilitate electron transfer in cellular metabolism.

Iron (Fe^{2+} or Fe^{3+}): Iron is a component of protein complexes like cytochromes and ferredoxins, which are responsible for electron transfer in the photosynthetic machinery of leaves. Iron is also involved in certain enzymes of the respiratory chain, such as cytochrome oxidase.

Copper (Cu^{2+}): Copper plays a similar role as iron in electron transfer mechanisms in the photosynthetic process.

Manganese (Mn^{2+}): Manganese is critical in the water oxidation system of Photosystem II in the photosynthetic machinery.

Boron (B): Boron deficiencies disrupt the transport of minerals and sugars within the plant.

Molybdenum (Mo^{2-}): Molybdenum is essential for the function of nitrate reductase, a key enzyme in nitrogen metabolism.

Zinc (Zn^{2+}): Zinc is essential for genetic expression, as it helps maintain the structure of transcription factors involved in regulating gene expression in plant cells.

Effect of Mineral Resource Availability on Growth

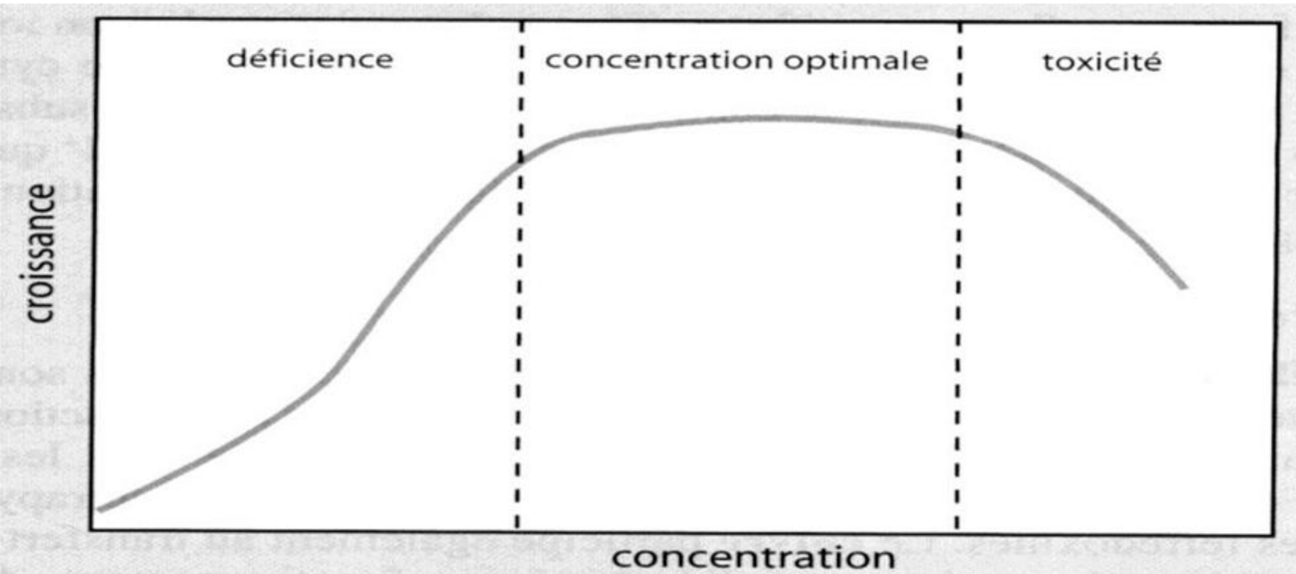


Figure: Influence of mineral element concentration on plant growth (Gaudy, 2012)

This curve illustrates an optimal plateau, with insufficiency at low concentrations and toxicity at high concentrations. Insufficiency can lead to nutrient deficiencies, while excess can cause toxicity.

Mineral Deficiency:

Manifestation: Mineral deficiency manifests as restricted growth, resulting in reduced yields. In the ascending part of the curve, the nutrient concentration in the environment is insufficient, which leads to a deficiency in the plant tissues and limits growth.

Critical Point: At the plateau of the curve, the concentration of the element is optimal. The minimum concentration of nutrients that allows for maximal growth is called the critical point.

Excess Nutrient Availability:

Luxury Consumption: Beyond the critical point, there is an increase in the concentration of the element in the vacuole that does not contribute to further growth. This is referred to as luxury consumption, where excess nutrients accumulate without benefiting the plant's development.

Toxicity: At higher nutrient doses, growth may slow down due to toxicity, which can occur when excessive amounts of certain minerals are absorbed.

Factors Influencing Ion Absorption by Plants:

The absorption of ions by plants depends on several factors, including:

Nature and Availability of Ions: The types of ions present in the soil and their interactions with each other play a crucial role in uptake.

Soil Characteristics:

Presence of Colloids: Charged colloids in the soil can affect ion retention and availability.

Soil Structure: The physical structure of the soil influences root penetration and nutrient absorption.

pH and Temperature: Slightly acidic soil solutions generally promote ion absorption. In contrast, extreme pH levels or unsuitable temperatures can hinder nutrient uptake.

Plant Factors:

Age and Physiological Condition: The ability of plants to absorb nutrients changes depending on their growth stage and overall health.

Biological Activity in the Rhizosphere: The microbial activity around plant roots (rhizosphere) also plays a role in nutrient uptake.

Impact of Soil pH on Nutrient Absorption:

Slightly acidic soil solutions are generally favorable for ion absorption by plants. However, the presence of excess calcium, which can alkalinize the soil, may disrupt the uptake of certain nutrients, such as iron. For example, in apple and grapevines, excess calcium can interfere with iron assimilation, leading to iron chlorosis — a deficiency in chlorophyll synthesis. This results in yellowing of the leaves, a typical symptom of ferric chlorosis.

Passive and Active Transport in Plants

The movement of an ion from one compartment to another, such as from the soil solution into the cytosol of a root hair, is referred to as passive transport when it occurs in the direction of a decrease in the concentration of that ion. Essentially, passive transport follows a concentration gradient, meaning that ions move from areas of high concentration to areas of low concentration.

On the other hand, active transport occurs when the concentration of the ion is higher in the receiving compartment than in the originating compartment. Active transport moves ions against their concentration gradient (from low to high concentration) and requires energy. This energy is typically provided by ATP (adenosine triphosphate), which powers the transport process.

Types of Transport Systems

There are various transport systems across the plasma membrane (cell membrane) and the tonoplast (vacuolar membrane) in plant cells, including:

Ion Pumps (ATPases):

H+ pumps (Proton Pumps): These pumps transport protons (H+) across membranes, typically out of the cell or into vacuoles, creating an electrochemical gradient. This is essential for processes like nutrient uptake and pH regulation.

Ca^{2+} ATPase pumps: These pumps actively transport calcium ions (Ca^{2+}) into the vacuole or out of the cytoplasm, helping regulate cellular calcium concentrations, which is crucial for signaling and cellular functions.

Transporters and Channels:

Ion Transporters: These proteins facilitate the movement of ions across membranes. Some are selective for particular ions, while others can transport a range of ions.

Ion Channels: These are pore-like structures in the membrane that allow ions to pass through passively (following their concentration gradient). Channels can be voltage-gated, ligand-gated, or mechanosensitive depending on what controls their opening.

Symport Systems:

Symport refers to the transport system where two different ions or molecules are transported in the same direction across a membrane. A well-known example is the H+/NO_3^- symport. In this system, protons (H+) are transported along with nitrate ions (NO_3^-), both into the cell, using the proton gradient established by proton pumps.

Antiport Systems:

Antiport refers to systems where two ions or molecules are transported in opposite directions across the membrane. A classic example is the H+/Na^+ antiport, where protons (H+) are pumped into the cell while sodium ions (Na^+) are pumped out. This system helps maintain ionic balance and regulate pH within the cell.

Summary of Transport Mechanisms:

Passive Transport: Movement of ions down their concentration gradient without energy expenditure (e.g., ion channels, diffusion).

Active Transport: Movement of ions against their concentration gradient, requiring ATP as an energy source (e.g., proton pumps, calcium ATPases).

These transport systems are essential for maintaining cellular homeostasis, nutrient uptake, and various physiological processes within plant cells.

5. Nitrogen Nutrition in Plants

Nitrogen, in both organic and mineral forms, constitutes about 1 to 5% of the dry matter of plants. It is primarily found in proteins, which typically contain about 16% nitrogen. Nitrogen is also present in other important biological molecules such as nucleic acids, coenzymes, vitamins, and hormones. When nitrogen is in its mineral form, it is present as ionic compounds such as NH_4^+ (ammonium) or NO_3^- (nitrate).

A. Atmospheric Nitrogen (N_2)

Proportion in Air: Nitrogen makes up approximately 78% of the Earth's atmosphere, making it the primary source of nitrogen.

Use by Plants: Despite being abundant, atmospheric nitrogen (N_2) cannot be directly used by most plants. Only certain plants, particularly those in symbiotic relationships with nitrogen-fixing bacteria (such as Rhizobium in legumes or cyanobacteria in some aquatic plants), are capable of converting atmospheric nitrogen into a form that plants can use.

B. Soil Nitrogen

Chemical Properties of Nitrogen: Nitrogen has five electrons in its outermost electron shell, three of which are unpaired, allowing nitrogen to form covalent bonds. The oxidation states of nitrogen can range from -3 (as in ammonium) to +5 (as in nitrate).

Forms of Soil Nitrogen: Nitrogen in the soil is available in several forms, including:

NO_3^- (Nitrate): The most common and mobile form of nitrogen in the soil.

NO_2^- (Nitrite): A transient form that results from the nitrification process.

NH_4^+ (Ammonium): A form of nitrogen that can be taken up by plants but is less mobile than nitrate.

Additionally, nitrogen can be found in organic forms, particularly in complex molecules such as proteins and amino acids, which are primarily found in humus in the soil.

Recycling of Nitrogen:

Decomposing organic matter, such as plant and animal residues, releases aminated compounds, which are broken down by microorganisms (mainly aerobic bacteria and some fungi). This process is known as mineralization, and it helps convert organic nitrogen into forms that can be used by plants.

Two Stages of Mineralization:

Ammonification: This stage produces ammonium (NH_4^+), and it is carried out by a wide variety of microorganisms, including bacteria.

Nitrification: This process converts ammonium into nitrate through two steps:

Nitrosation: The first step is the conversion of ammonium (NH_4^+) into nitrite (NO_2^-) by Nitrosomonas bacteria.

Nitratation: In the second step, Nitrobacter bacteria convert nitrite (NO_2^-) into nitrate (NO_3^-), which is a form of nitrogen that plants can readily absorb.

Denitrification: Denitrification is another key process in the nitrogen cycle, in which ammonium (NH_4^+) is converted back into gaseous nitrogen (N_2) by denitrifying bacteria. This process can occur in anaerobic conditions and results in the release of nitrogen back into the atmosphere, completing the nitrogen cycle.

The Nitrogen Cycle

Nitrogen Fixation: Atmospheric nitrogen (N_2) is converted into ammonium (NH_4^+) or nitrate (NO_3^-), either by symbiotic bacteria (like in legumes) or by free-living nitrogen-fixing bacteria.

Mineralization: Decomposition of organic matter releases nitrogen in the form of ammonium (NH_4^+).

Nitrification: Ammonium (NH_4^+) is converted to nitrite (NO_2^-) and then to nitrate (NO_3^-), which is usable by plants.

Denitrification: Under anaerobic conditions, nitrates (NO_3^-) are reduced back to gaseous nitrogen (N_2), completing the cycle.

Summary

Nitrogen is essential for plant growth and is primarily found in proteins, amino acids, and nucleic acids.

Plants absorb nitrogen mainly in the forms of nitrate (NO_3^-), ammonium (NH_4^+), and nitrite (NO_2^-).

The soil's nitrogen content is replenished through mineralization, which involves ammonification and nitrification.

The nitrogen cycle involves processes like nitrogen fixation, mineralization, nitrification, and denitrification, which recycle nitrogen in ecosystems.

This complex cycle ensures that plants have continuous access to nitrogen, a crucial nutrient for their growth and development.

Reduction of Nitrates in Plants

In plants, nitrate (NO_3^-), which is absorbed from the soil, undergoes a series of reductions before it can be incorporated into organic compounds such as amino acids and proteins. This process primarily takes place in the roots and leaves. Here’s how the reduction of nitrate occurs:

1. Nitrate Absorption in Roots

Active Transport: Nitrate is absorbed by the plant's roots through active transport mechanisms. This process requires energy to move nitrate from the soil into the root cells against its concentration gradient.

Proton Gradient and ATPase Pumps: The energy needed for this process comes from the proton gradient generated by the ATPase proton pumps (also called H^+-ATPases). These pumps actively transport protons (H^+) out of the root cells, creating a proton gradient across the cell membrane. This gradient helps drive the influx of nitrate (NO_3^-) into the cell via specific nitrate transporters.

Similar Mechanism in Leaves: A similar mechanism also exists in the leaves, where nitrate is transported into leaf cells to support processes like protein synthesis and amino acid formation.

2. Nitrate Reduction to Nitrite (NO_2^-)

Once inside the plant cells, nitrate undergoes a reduction process. This reduction takes place in two steps:

Nitrate Reductase (NR): The enzyme nitrate reductase (NR) catalyzes the first reduction step, converting nitrate (NO_3^-) into nitrite (NO_2^-). This reaction also requires the input of electrons, which are typically provided by NADH or NADPH. Nitrate reductase is located in the cytoplasm and can be regulated by the plant's nitrogen status.

Nitrite Reductase (NiR): The nitrite reductase (NiR) enzyme then reduces nitrite (NO_2^-) into ammonium (NH_4^+). This step takes place in the chloroplasts (in green tissues like leaves) or plastids in non-green tissues. This reduction also requires electrons, typically provided by ferredoxin, a protein that carries electrons from the light-dependent reactions of photosynthesis.

3. Incorporation into Amino Acids

Ammonium (NH_4^+), once produced, is either directly used by the plant in the synthesis of amino acids and other nitrogenous compounds or is incorporated into organic molecules like glutamine and glutamate through the glutamine synthetase/glutamate synthase cycle.

Excess ammonium (NH_4^+) can be toxic to plants, so it is typically stored in the vacuole or converted into amino acids to prevent toxicity and make it available for future biosynthetic needs.

Summary of Nitrate Reduction Process

Absorption of Nitrate: Nitrate (NO_3^-) is actively transported into root cells using the energy from a proton gradient created by ATPase proton pumps.

Nitrate Reduction to Nitrite: In the cytoplasm, nitrate reductase (NR) reduces nitrate to nitrite (NO_2^-).

Nitrite Reduction to Ammonium: In the plastids (especially in chloroplasts in leaves), nitrite reductase (NiR) reduces nitrite to ammonium (NH_4^+).

Incorporation into Organic Molecules: Ammonium is then incorporated into amino acids and other nitrogenous compounds, crucial for the plant's growth and metabolism.

This entire process is vital for plants to convert inorganic nitrogen (NO_3^-) from the soil into organic nitrogen forms that can be used in building proteins, enzymes, and other essential biomolecules.

Assimilation of Ammonium (NH_4^+)

The ammonium ion (NH_4^+) is incorporated into organic molecules (such as amino acids, nitrogenous bases, etc.). This incorporation involves the enzyme glutamine synthetase (GS), which catalyzes the following reaction:

$NH4^+ + glutamate + ATP \rightarrow glutamine + ADP + Pi$

In the presence of ammonium ions and ATP, glutamine synthetase (GS) converts a molecule of glutamate into glutamine (Gln).

Symbiotic Nitrogen Fixation

Several symbiotic nitrogen-fixing associations are known, with the most well-known example being the association between bacterial species and legumes. The most common form of symbiotic association leads to the formation of multicellular hypertrophied structures, called nodules, on the root of the host plant.

6. Carbon Nutrition (Photosynthesis)

Photosynthesis is a physiological process by which plants containing certain pigments (particularly chlorophyll) capture light energy and convert it into chemical energy to produce carbon-based nutrition from atmospheric CO_2. This process is accompanied by the release of oxygen.

Plants synthesize their organic matter from simple molecules ($CO_2 + H_2O$) and light energy (sunlight), where CO_2 and water combine (reduction reaction) to form carbohydrates.

The general formula for photosynthesis is:

$CO2 + H2O + h\nu$ (light energy) $\rightarrow (CH2O) + O2$

Location

In green plants, the photosynthetic machinery is mainly located in the leaves. Leaf chlorophyll cells contain several hundred chloroplasts. Depending on the species, each cell may have between 10 and 100 chloroplasts (the more chloroplasts, the smaller they are). Chloroplasts are typically found in leaves, but also in petioles, herbaceous stems, and some floral organs.

The chloroplast is a double-membraned organelle, oval in shape and a few tens of micrometers in length. The outer membrane is relatively permeable and continuous, while the inner membrane is impermeable (a selective barrier), folded into sacs (thylakoids) where pigments are located.

The chloroplast is composed of grana and stroma. The granum is a stack of thylakoid sacs, each consisting of 2 to 100 disks, connected by stroma lamellae, forming a continuous network. The stroma also contains ribosomes and circular DNA.

Photosynthesis takes place in two main phases : Light and Dark Phases

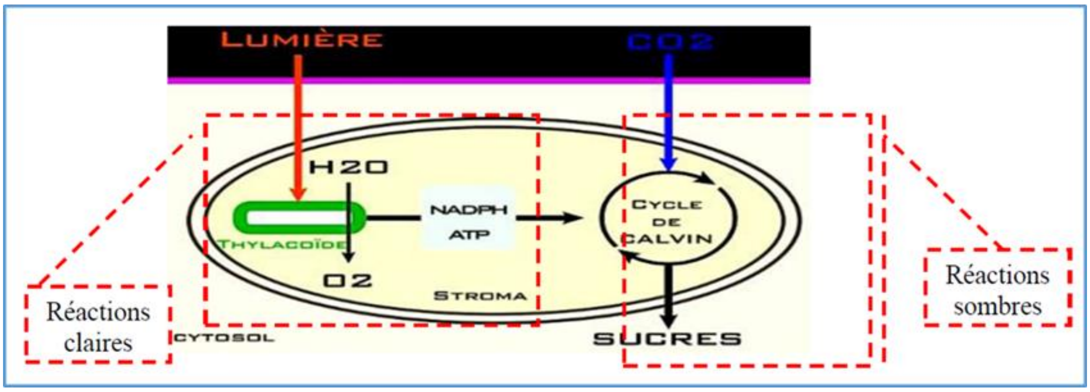
I. The Light Phase (Photochemical Reactions)

These are the steps that convert solar energy into chemical energy. Light triggers the transfer of electrons and protons, and the photochemical reactions occur within the thylakoids.

II. The Dark Phase (Calvin Cycle)

This phase is the carbon fixation phase, during which CO_2 is incorporated and then reduced to produce a carbohydrate.

The Calvin cycle takes place in the stroma of the chloroplasts.



The Synthesis of Energy Molecules NADPH and ATP, Resulting from the Conversion of Light into Chemical Energy, Requires the Functioning of Photosystems

I. The Light Phase (Photochemical Reactions)

What is a Photosystem?

Photosystems are complexes of proteins and pigments that capture and convert light energy into chemical energy at the thylakoid membrane. They consist of antenna complexes and a reaction center.

The antenna is made up of pigments (chlorophylls and carotenoids). Each pigment molecule absorbs a photon, which excites it to a higher energy state. This excitation is then transferred from one chlorophyll molecule to another through resonance (without energy transformation).

The excitation is eventually passed to a specific chlorophyll "a" molecule, which is associated with the reaction center. This chlorophyll molecule is excited and transfers an electron to a primary electron acceptor. After reduction, this acceptor passes its electron to a secondary acceptor, and the process continues along the electron transport chain.

Two Types of Photosystems

There are two types of photosystems in the thylakoid membrane.

1. Photosystem II (PSII)

Light energy is first absorbed by the light-harvesting antenna, which then transfers its energy to the P680 complex. The chlorophyll "a" molecule in the P680 complex then releases an electron, which is captured by the primary electron acceptor (chlorophyll A_0 = modified chlorophyll "a") and transported through the electron transport chain (pheophytin, quinone, and plastoquinone).

This electron then passes through the cytochrome complex, where it induces the movement of protons from the stroma into the thylakoid lumen. These accumulated protons create what is known as the proton gradient, which allows ATP synthase to produce ATP (phosphorylation). After leaving the cytochrome complex, the electron is transferred to Photosystem I (PSI).

At the level of PSII, the chlorophyll "a" in P680 has lost electrons (photo-oxidized), and these electrons must be replenished via the photolysis of water — a non-cyclic electron transport. Water is, therefore, the primary electron donor in photosynthesis. The reaction is as follows :

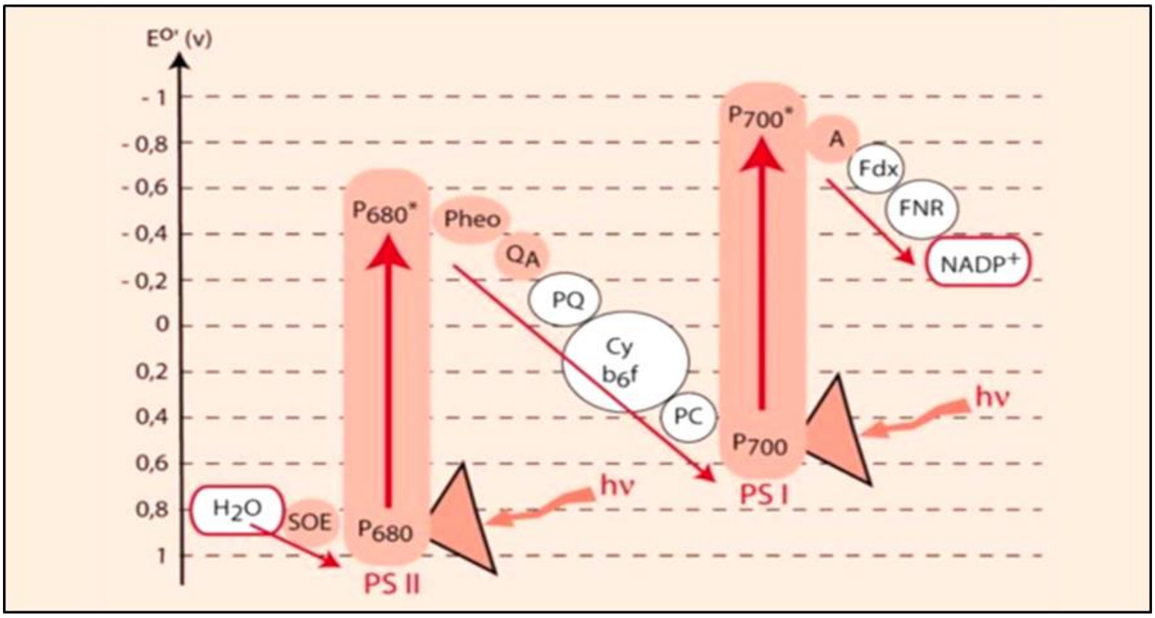
$$\frac{1}{2} H_2O \rightarrow \frac{1}{2} O_2 + H^+ + 1\ e^-$$

The electron released during the photolysis of water is captured by PSII, the protons produced accumulate in the thylakoid lumen to participate in the proton gradient, and the oxygen is released into the atmosphere. Therefore, oxygen is a byproduct of photosynthesis.

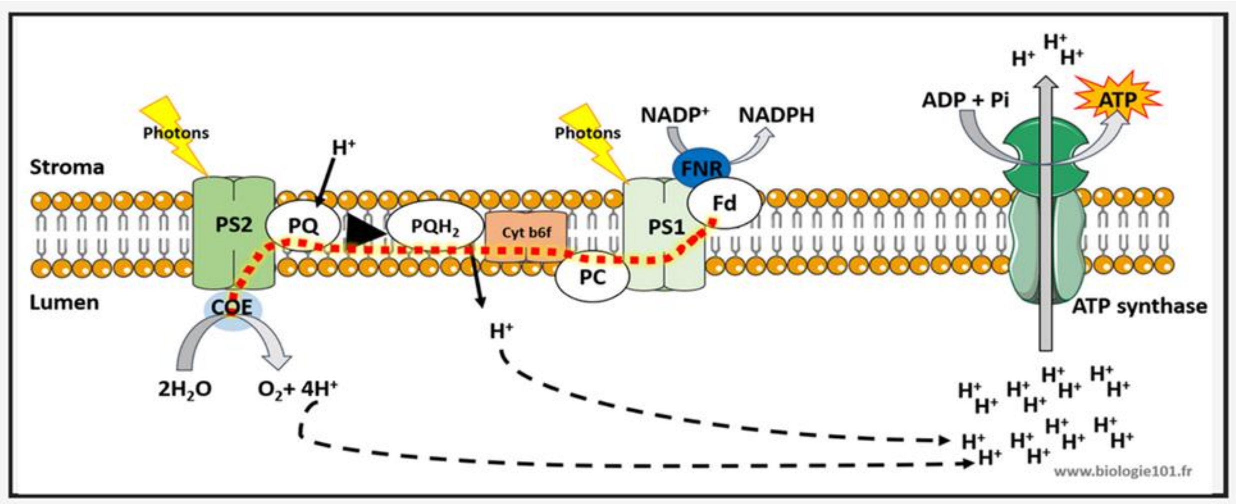
2. Photosystem I (PSI)

The continuation of photosynthesis still requires light energy, which is absorbed by the light-harvesting antenna of PSI and transferred to the P700 complex. The chlorophyll "a" molecule in the P700 complex then releases an electron, which is transported through the electron acceptor chain until it reaches ferredoxin. The reduced ferredoxin then transfers the electron via ferredoxin-$NADP^+$ reductase (FNR) to oxidized $NADP^+$, reducing it to NADPH.

The chlorophyll "a" in P700 has thus lost an electron, which it must recover in order for the system to continue functioning. This electron is provided by PSII through the electron carrier plastocyanin.



Z-Scheme of Electron Transfer



The Light Phase

II. The Dark Phase - Biochemical Phase (The Calvin Cycle)

This phase occurs simultaneously with the light-dependent phase, but it does not require light energy. The biochemical phase allows for the fixation of carbon from atmospheric CO2 and binds it to the hydrogen atoms of water molecules.

CO2 Fixation

The first molecule of the Calvin cycle is ribulose bisphosphate (RuBP), also known as RuDP, which contains five carbon atoms. The fixation of CO2 onto this molecule requires the enzyme Rubisco (Ribulose Biphosphate Carboxylase Oxygenase). This enzyme facilitates the formation of an unstable six-carbon molecule, which quickly splits into two molecules of 3-phosphoglycerate (3-PGA), each containing three carbon atoms.

Reduction of the Fixed Carbon

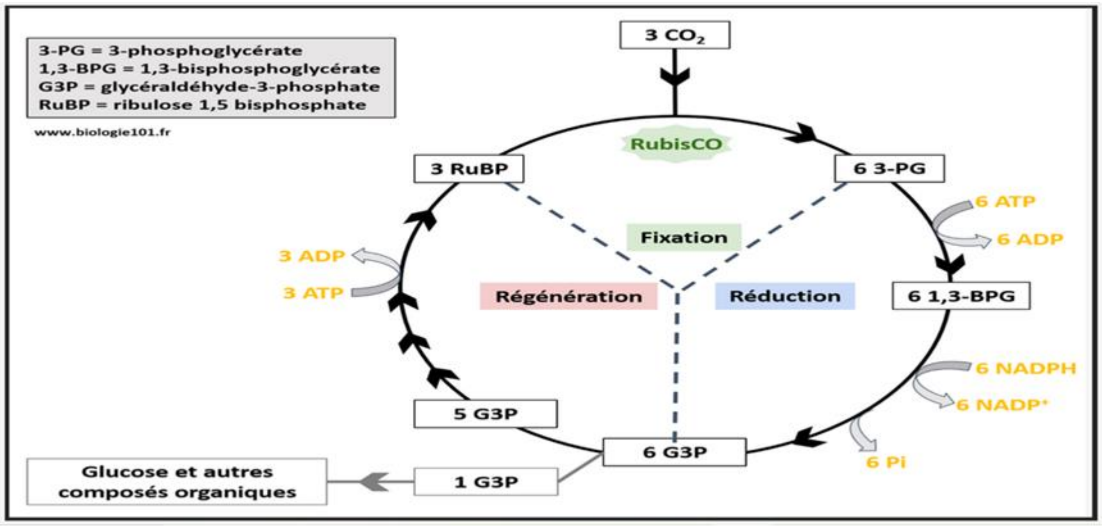
The second phase of the Calvin cycle involves the reduction of 3-phosphoglycerate. This molecule is first phosphorylated by ATP to form 1,3-bisphosphoglycerate, which is then reduced by NADPH to form glyceraldehyde-3-phosphate (G3P), also known as PGAL. G3P is a sugar and represents the primary product of the cycle.

Regeneration of the CO2 Acceptor

The G3P formed can have several fates. One-sixth of it will be used by the cell as a sugar component, while the remaining five-sixths will be used to continue the Calvin cycle.

The regeneration of RuBP, which will be reused to fix CO2, involves several steps and requires ATP.

Glyceraldehyde-3-phosphate produced in the chloroplast is quickly transported to the cytoplasm, where it contributes to the synthesis of sucrose.



Different Types of Carbon Fixation

There are three known mechanisms for carbon dioxide fixation during photosynthesis : C3, C4, and CAM. These three mechanisms differ in the efficiency of this process. The C3 mechanism is the "basic" mechanism and is found in 98% of green plants. C4 and CAM mechanisms are rarer but are found in well-known species : maize is a C4 plant, and pineapple is a CAM plant. These mechanisms are adaptations to water stress or reduced CO2 availability during the day.

The first step of the Calvin cycle is a carboxylation (the fixation of one molecule of CO2) onto ribulose 1,5-bisphosphate, catalyzed by Rubisco, resulting in two molecules of a three-carbon compound (3-phosphoglyceric acid, PGA). However, this enzyme can also catalyze reactions between oxygen and RuBP (oxygenase activity), which leads to photorespiration. This process blocks the cycle. Photorespiration occurs when CO_2 concentrations in the chlorenchyma are too low. However, Rubisco has a stronger affinity for CO_2 than for O_2.

The problem of stomatal closure in a hot and dry atmosphere, leading to a lack of CO_2 in the chlorenchyma, is solved by C4 plants, such as maize or sugarcane. In these plants, mesophyll cells use PEPase (phosphoenolpyruvate carboxylase) to fix CO_2 onto a three-carbon compound (phosphoenolpyruvate), producing an unstable four-carbon compound, malate. This malate is then transported to the vascular bundles, where it is decarboxylated to produce pyruvate, releasing CO_2, which enters the Calvin cycle.

The CAM (Crassulacean Acid Metabolism) mechanism differs from C4 in that carbon fixation is not separated spatially but temporally (night/day). During the night, when the stomata are open, a stock of malate is produced and stored in the vacuoles of the photosynthetic cells. During the day, these malates are converted back into CO_2, allowing the Calvin cycle to occur, with the CO_2 remaining available for photosynthesis despite the stomatal closure. This mechanism helps to limit water loss through transpiration. It is notably observed in Crassulaceae (succulent plants), such as cacti.