The path of carbon in photosynthesis

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How is the carbon from carbon dioxide - CO_2 - present in the atmosphere integrated into the organic matter that makes up living organisms, the biomass? For several billion years, this process has been carried out during the biochemical stages of photosynthesis by organisms using the energy recovered from sunlight

by chlorophyll. However, photosynthesis has had to adapt these mechanisms to survive the various environmental changes that have taken place over geological time scales. The accumulation -in the atmosphere- of oxygen (O_2) produced during the photochemical stages of photosynthesis (see Shedding light on Photosynthesis) was one of these major events. Different original strategies have been adopted over the course of evolution, and have thus made it possible to produce an immense biodiversity of organic biomolecules that we use for food, heating, clothing, housing and health care.

1. What is photosynthesis?

1.1. Making biomass from CO_2 in the air

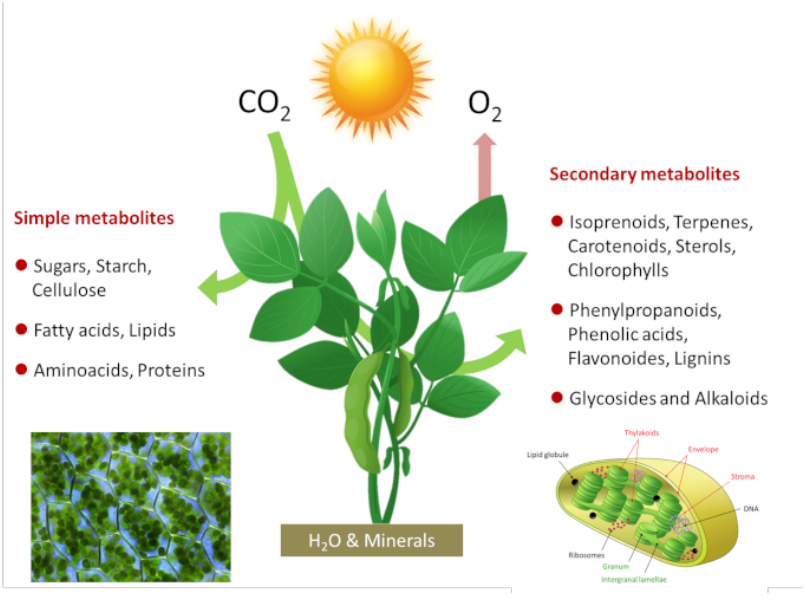

Figure 1. Photosynthesis, source of biomass and oxygen. Simplified diagram representing the main reactions of photosynthesis, the products (metabolites) that result and the cellular organelles rich in lamellar systems: chloroplasts, the site of photosynthesis. [Source: © Jean-François Morot-Gaudry]

Photosynthesis, a very ancient mechanism (3.8 billion years), brings together a **set of biophysical and biochemical reactions** that allow chlorophyll-containing **plants**, algae and photosynthetic bacteria to **synthesize organic molecules** using the electromagnetic energy of **sunlight**, carbon from **CO_2** in the **air**, **water** and **minerals in the soil** (Figure 1).

Photosynthetic organisms are therefore photoautotrophic*. Photosynthesis is at the origin of most of the molecules in the **food chain** of living beings and the majority of the organic **biomass** of our Planet. Photosynthesis takes place in **chloroplasts**, green intracellular organelles a few micrometers in size that contain the photosynthetic machinery (see Shedding light on Photosynthesis). The simplified equation for photosynthesis can be written as follows:

$CO_2 + H_2O$ + light energy → energy-rich carbon molecules + O_2

Photosynthesis fixes 115 to 120 billion tons (or Gigatons) of carbon each year from CO_2 in the air, including 60 for the continents. To achieve this, plants use a very small part (about 1-2%) of the solar energy reaching our planet. On a global scale a power of about 130-140 terawatts (1 terawatt = 10^{12} watts) is used, which is about six times the energy consumption of mankind. How do photosynthetic organisms achieve this?

1.2. Photosynthesis is divided into two phases

a very fast **photochemical phase** that takes place in the membrane system of the chloroplasts, the **thylakoids** (Figures 1 & 2).

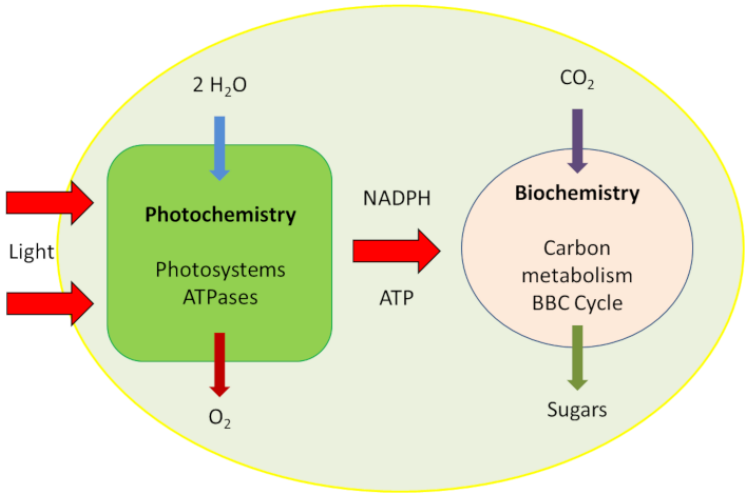

Figure 2. The two phases of photosynthesis (i) the photochemical phase: production -from sunlight energy- of NADPH reducing power and ATP; (ii) and the biochemical phase: fixation of CO2 carbon and synthesis of organic compounds: carboxylation and Benson-Bassham-Calvin Cycle (BBC cycle). [Source: © Jean-François Morot-Gaudry]

During this phase, visible solar **light** is **captured** by the chlorophyll **pigments** of the chloroplasts. The energy acquired is then transmitted to protein/pigment complexes (**photosystems**) which **convert**, *via* a succession of oxidation-reduction reactions, the **energy of** the **photons** into **electrical** and then **chemical** energy stored in the form ofboth organic **molecules rich in energy** and **reducing power** (NADPH). Simultaneously, the establishment of a proton gradient on either side of the thylacoid membrane provides the energy necessary for **ATP synthesis**. During this process, water molecules -H_2O- are the source of electrons (e^-), protons (H^+) and oxygen (O_2). This phase is thoroughly described in this encyclopedia (see Shedding light on Photosynthesis).

A **metabolic phase,** slower than the previous one, takes place in the inner liquid of the chloroplasts, the stroma (Figure 2).

The biochemical mechanisms involved in the **fixation of carbon** from the **CO_2** of the air require the presence of a carbon receptor: an **enzyme** that ensures this fixation and **carboxylation**, giving rise to organic compounds. This photosynthetic carbon metabolic pathway is known as the **Benson-Bassham-Calvin Cycle**.

This article focuses primarily on the description :

the biochemical mechanisms of photosynthesis responsible for the fixation of carbon from carbon dioxide in the atmosphere ;

of their evolution during changes in the environment;

the impact of the appearance of oxygen in the atmosphere during different geological periods.

2. How do plants fix carbon from CO_2?

2.1. Some history

Jean Sénebier (see Focus Some pioneers in photosynthesis) was the first scientist having stated -as early as 1782- "*that carbon dioxide CO_2 is fixed under illumination by photosynthetic organisms and represents food for the plant*". From the late 18th century to the mid-1940s, the nature of the photosynthetic pathways for the assimilation of carbon from carbon dioxide (CO_2) remained a mystery. It was first assumed -in the early 19th century- by J.B. Boussingault and F. Bayer, that carbohydrates could result from the combination of carbon with the elements of water, hence the first name carbohydrates was given to sugars. Most formulas representing sugars can in fact be inscribed as if they were the result of the polymerization of this fundamental molecule containing carbon and water: $(CH_2O)n$. Subsequently, several other compounds were mentioned as the first products of photosynthesis. Examples include carbonic acid H_2CO_3, formic acid HCOOH, the simplest of the carboxylic acids*, etc. However, there were no experimental results to confirm these hypotheses. If the hypothesis of formic acid has been maintained for a very long time in the literature as the first product of photosynthesis, it owes this only to its disarming simplicity.

2.2. The Benson-Bassham-Calvin Cycle

Search for CO_2 acceptor and discovery of a specific carboxylase

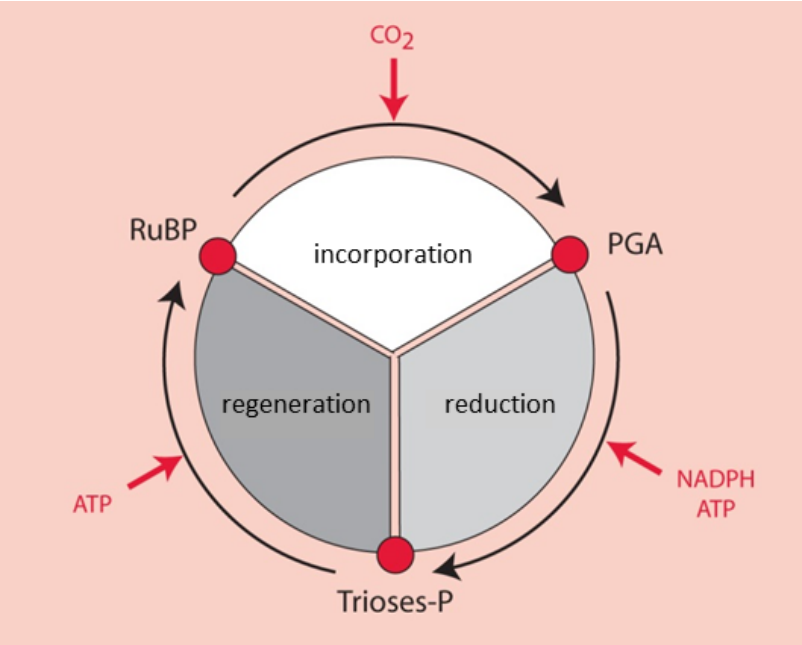

Figure 3. Simplified diagram of the Benson-Bassham-Calvin cycle. Representation of the steps of incorporation and reduction of the photosynthetic carbon leading to the formation of PGA phosphoglyceric acid and triose-phosphates, first photosynthetic intermediates, and to the regeneration of the CO2 acceptor, ribulose-1,5-bisphophate. [Source: Schéma Roger Prat, in Morot-Gaudry, Dunod, 2009]

First experiments using the radioactive isotope $^{11}CO_2$ [1] as a marker, showed that the ^{11}C carbon was found in a three-carbon compound, suggesting that the carbon acceptor of CO_2 was a two-carbon compound. But this hypothetical compound couldn't be identified.

It was by using $^{14}CO_2$ as a radioactive tracer that Benson [2] observed that the **carbon of $^{14}CO_2$ binds to** a more complex pre-existing carbon structure: **a five-carbon phosphoryl compound**, ribulose-1,5-bisphosphate or **RuBP** (see Focus on Deciphering the Benson-Bassham-Calvin Cycle). [3] This compound has a chemical structure favourable to the addition of a carbon (a reaction called carboxylation). This reaction results in the formation of a very unstable six-carbon compound, which is immediately metabolized into two three-carbon (C3) molecules, phosphoglyceric acid, **PGA** [4] (Figure 3).

The enzyme that binds the CO_2 carbon to RuBP is a carboxylase*, RuBP carboxylase, later called RubisCO (see below). This specific enzyme of photosynthesis has been the **gateway for carbon** to enter the majority of the planet's **organic molecules** for more than **three billion years** (see Focus RubisCO).

RubisCO, a complex enzyme of high molecular weight (550 kDa) [5], is localized in the stroma of chloroplasts where it accounts for 30-50% of soluble proteins. RubisCO is the most quantitatively important enzyme in the biosphere, and is thus the main reserve of organic nitrogen in leaves [6]. Because of its central role in autotrophy, it is considered that the presence on Earth of each human being required the formation of 5 kg of RubisCO.

Reduction of phosphoglyceric acid to triose-phosphates

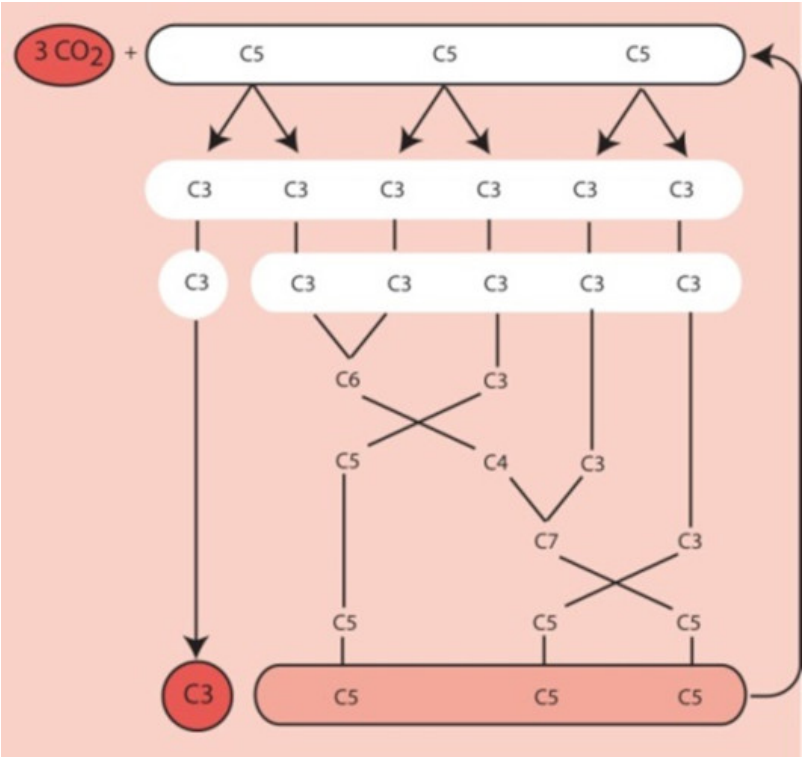

Figure 4. Simplified diagram of the Benson-Bassham-Calvin Cycle with carbon trading. Phosphorylation reactions are not indicated, only the number of carbons in the molecules is shown [Source: © Schéma Roger Prat, in Morot-Gaudry, Dunod, 2009].

Recovering the energy of the NADPH reducing power and of ATP from the photochemical phase (see Shedding light on Photosynthesis), the three-carbon **PGA** molecules are **reduced** (they gain electrons) into **triose-phosphate** molecules (molecules with 3 carbons and a phosphate) and thus acquire energy. This enzymatic reduction requires one NADPH molecule and one ATP molecule per reduced PGA molecule.

Fate of triose-phosphate

For **six molecules of triose-phosphate** synthesized, **only one is intended for the synthesis of carbohydrates, amino acids, lipids**, etc. The **other five** molecules of trioses-phosphate are used to **regenerate RuBP**, the CO_2 acceptor (Figure 4). The regeneration of a RuBP molecule has a high energy cost that requires 2 NADPH and 3 ATP per molecule but this energy is provided free of charge by the Sun.

Since the first products of this ring are three-carbon molecules, the plants using this ring have been called **C3-type photosynthetic plants**.

Trioses-phosphate that are not used for RuBP recycling are either (a) used in the chloroplast for the synthesis of starch, amino acids or lipids or (b) exported out of the chloroplast and transformed into sugars by the enzymes of the cytoplasm for further metabolism (see Focus Sucrose or Starch?).

Synthesis and transport of photosynthetic assimilates

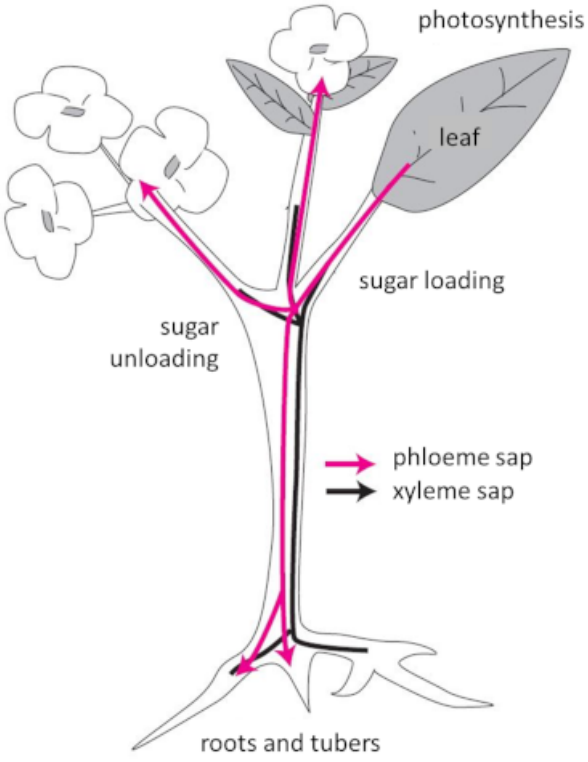

Figure 5. Circulation of raw and phloem sap in the plant. [Source: © Jean-François Morot-Gaudry]

The products of photosynthesis, the assimilates, are transported and distributed throughout the plant by the conductive system that conducts the elaborated sap -the phloem-, which is parallel to the system that conducts the raw sap, the xylem (Figure 5). The long-distance transport of the phloem sap requires that the assimilates (sucrose, mainly amino acids) synthesized in the source organs, the leaves, are loaded into the conducting complex by an active and selective loading mechanism, then continuously discharged into the receiving organs: grains, seeds, fruits, tuberized roots and stems, etc.

2.3. What about temperature?

Temperature affects biophysical and metabolic processes differently. Biophysical processes such as light absorption by chlorophyll pigments and the formation of NADPH and ATP are not very sensitive to temperature changes. On the other hand, the biochemical reactions that cause CO_2 and O_2 fixation and sugar synthesis, as well as the exchange of molecules between cell compartments and organs, are highly dependent upon it. On average, a 10°C rise in temperature doubles the velocity of biochemical reactions.

In temperate regions, air and plant temperatures are subject to strong seasonal and daily variations that are parallel to the amount of solar energy reaching the ground surface. Plants can, to varying degrees, adapt to rapid daily variations in temperature, between morning and end of day for example. Rapid changes in leaf temperature usually follow variations in sunlight. In environments characterized by low temperatures, such as the alpine environment, plants have developed mechanisms that allow them to cope with these temperature variations (see How do plants cope with alpine stresses?).

Plants can also acclimatize to long-term temperature changes. In all cases, the temperature at which maximum photosynthetic activity is observed follows the growth temperature. Acclimatization to new thermal conditions can nevertheless cause a decrease in photosynthesis in some plants.

3. Oxygen production over geological times

The first **photosynthetic reactions** appeared more than **three billion years** ago when the **atmosphere** was almost **devoid of dioxygen** O_2 but composed mainly of water (H_2O), carbon dioxide CO_2 (10 to 15%), nitrogen dioxide (N_2), and hydrogen sulfide (H_2S). At that time, during the transformation of light energy into energy-containing molecules**,** primitive photosynthetic bacteria - the purple **sulphurous bacteria** like the green sulphurous bacteria - **oxidized hydrogen sulphide**. **Photosynthesis** was of an **anoxygenic** type.

With the appearance of the ancestors of **cyanobacteria**, **H_2O** became the almost inexhaustible **substrate** for oxidation and the supplier of electrons and protons leading to **oxygen release** into the atmosphere. **Photosynthesis** became of the **oxygenic** type (see Shedding light on Photosynthesis). Presently, these two types of photosynthesis coexist:

$CO_2 + 2\ H_2S \rightarrow (CH_2O) + H_2O + 2\ S$ (Anoxygen photosynthesis)

$CO_2 + 2\ H_2O \rightarrow (CH_2O) + H_2O + O_2$ (Oxygenic photosynthesis)

After the onset of oxygen-source photosynthesis about 2.5 billion years ago, the concentration of O_2 in the atmosphere remained very low for a very long period of time due to the high capacity of crust minerals to trap oxygen in the form of iron oxide (Fe_2O_3). This phase in the Earth's history is clearly marked in the red geological layers rich in this iron compound (see The Biosphere, a major geological player). After all the minerals were saturated by oxygen, *i.e.* after the "great oxidation" period that took place about 2.4 billion years ago, the level of oxygen released by the photosynthetic activity of cyanobacteria and eukaryotes strongly increased in the atmosphere. At concentrations close to 21% of the gaseous concentration in the atmosphere, the oxygen content has become a serious issue for photosynthetic species.

4. Oxygen, a catastrophe for photosynthesis?

4.1. More history

In the 1920s, Otto Warburg [7] observed that if the oxygen O_2 content of the air (currently 0.0408% CO_2) [8] is lowered by 20 to 2%, the net rate of CO_2 assimilation is multiplied by a factor of 1.5 to 2. This is the so-called Warburg effect: high **oxygen** tensions **inhibit carbon dioxyde uptake under illumination**. In the 1970s, following labelling experiments using the oxygen isotope ^{18}O, Bowes, Lorimer, Ogren and Tolbert showed that **ribulose biphosphate carboxylase**, the enzyme that binds carbon dioxide, is **also capable of binding oxygen**. [9]

4.2. Dilemma for the RubisCO: the O_2/CO_2 competition

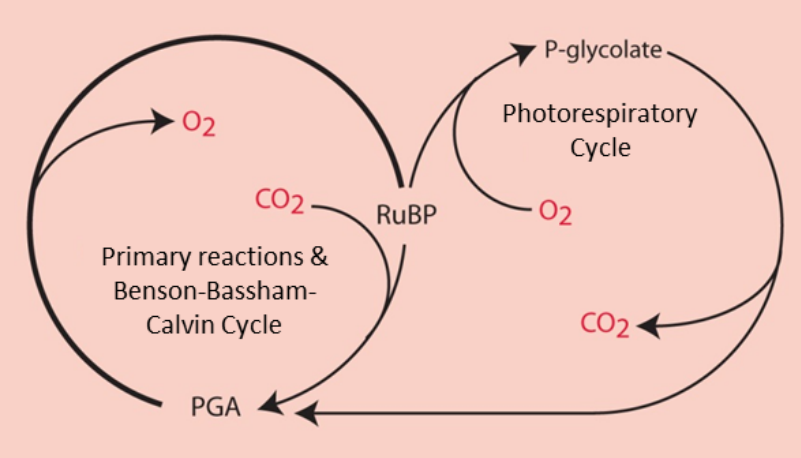

Figure 6. Relationship between the photosynthetic cycle and the photorespiratory cycle. PG, phosphoglycolate; PGA, 3-phosphoglycerate; RuBP, ribulose-1-5 bisphosphate. Photorespiration is therefore a catabolic mechanism: it consumes oxygen and releases CO2, leading to a loss of photosynthetic substrates. During this process, CO2 is released, but the reactions involved bear no resemblance to those of classical mitochondrial respiratory metabolism. [Source: Schéma Roger Prat, in Morot-Gaudry, Dunod, 2009]

Ribulose biphosphate carboxylase thus exerts in addition to its carboxylase activity a second activity called oxygenase, hence the name RubisCO (Ribulose bisphosphate Carboxylase Oxygenase) attributed to this bifunctional enzyme (Figure 6). **CO_2 and O_2 are then in competition at the catalytic sites of the RubisCO** and are involved in two antagonistic activities within the same molecule:

Carbon dioxide promotes the carboxylase function of the RubisCO ;

Dioxygen promotes the oxygenase function through a process called photorespiration.

In the presence of a **high concentration of CO_2**, **RubisCO functions** only as a **carboxylase** leading to the **synthesis of** two **PGA** molecules (C3 molecules), which are the origin of the phosphorylated sugars formed by the Benson-Bassham-Calvin ring.

RuBP (C5 molecule) + CO_2 (C1 molecule) → 2 PGA (C3 molecule) (carboxylation reaction)

On the other hand, in the presence of a **high concentration of O_2** and a **low concentration of CO_2**, RubisCO gives rise to a **PGA** molecule (C3 molecule) and a molecule with two carbon atoms, the phosphoglycolate (or **P-glycolate**).

RuBP (C5 molecule) + O_2 → PGA (C3 molecule) + P-glycolate (C2 molecule) (Oxygenation reaction)

4.3. The 2P-glycolate Cycle

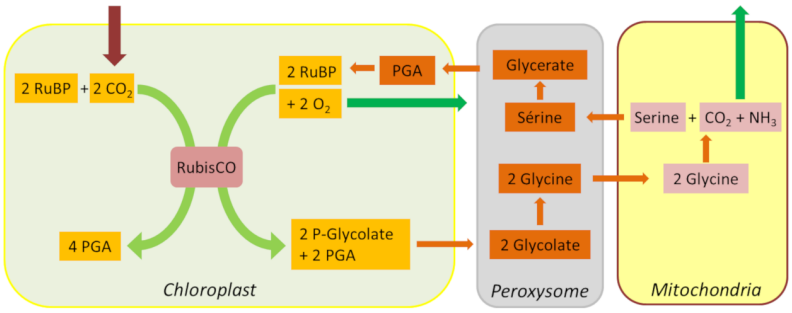

Figure 7. The 2P-glycolate cycle includes three different cellular organelles: chloroplasts, peroxisomes and mitochondria. Two molecules of 2P-glycolate formed in chloroplasts during photorespiration are dephosphorylated into two glycolate molecules, which are transferred into peroxisomes and aminated into two glycine molecules metabolized into one serine molecule, NH3 and CO2, the latter returning to the atmosphere. The remaining serine returns to the peroxisomes where it is metabolized to glycerate and finally to PGA in the chloroplast, reintegrating the Benson-Bassham-Calvin cycle. [Source: © Jean-François Morot-Gaudry]

The first product of photorespiration, **2P-glycolate** has been shown to be a powerful **inhibitor of the Benson-Bassham-Calvin cycle**. The majority of plants got rid of this toxic compound by metabolizing it via a complex pathway, the 2P-glycolate cycle (also known as the oxidative photosynthetic carbon cycle or Tolbert cycle), which involves the cooperation of three cellular organelles, the chloroplast, the peroxisome* and the mitochondrion*. [10] During this cycle, two molecules of 2P-glycolate are transformed into a PGA molecule reintegrated into the Benson-Bassham-Calvin Cycle, while one molecule of CO_2 and one molecule of ammonia (NH_3) are emitted into the atmosphere.

In addition to these carbon and nitrogen losses, glycolate recycling also has a significant energy cost in NADPH and ATP. However, thanks to the unfolding of the glycolate pathway, a large part of the carbon from photorespiration is eventually recovered, thus limiting the loss of photosynthetic carbon (Figure 7).

Photorespiration is mainly expressed in **plants** growing in **temperate regions** (wheat, barley, tomato, lettuce, potato, trees), photosynthetic plants of type C3. It is estimated that at 25°C, under normal environmental conditions, *i.e.* 21% oxygen and 0.0408% CO_2, the ratio between carboxylation and oxygenation rates is about 2.5, *i.e.* the emission of photorespiratory CO_2 corresponds to about a 20% loss of photosynthetic CO_2 assimilation. The importance of photorespiration is very much linked to environmental conditions:

Photorespiration is all the more important as the temperature and the illumination are high and the CO_2 content of the atmosphere is low;

Conversely, high CO_2 concentrations favour carboxylation.

4.4. Photorespiration: a major adaptive process

For more than 3 billion years, photosynthesis, a very robust process, has been very stable while adapting to the major environmental changes that the planet has undergone (see The Biosphere, a major geological player). The evolution of photosynthetic metabolism is tightly associated with changes in the environment:

As the oxygen content of the atmosphere increased, the CO_2/O_2 ratio decreased dramatically and caused global glaciation about 700 million years ago.

These new conditions induced a high oxygen pressure on the functioning of RubisCO in microorganisms and algae, prior to the colonization of the continents. [11]

Adapting to these new conditions, the branch of the green lineage (ancestor of terrestrial plants) developed the photorespiratory pathway, which in turn enabled the subsequent colonization of the continents, some 430 million years ago.

Once in the open air, plants have had to cope with this new evolutionary pressure and have sought to reduce or bypass photorespiration by different strategies.

Photorespiration is thus an inevitable photosynthetic process because it is linked to the intrinsic properties of the RubisCO itself that formed during evolution at a time when the oxygen content of the environment was almost negligible [12].

5. Concentrating CO_2 in the vicinity of the RubisCO

Apart from C3 plants, several other photosynthetic organisms (cyanobacteria, C4 and CAM plants...) have developed original strategies to effectively reduce the harmful effects of oxygen on RubisCO. One of the most ovious was to concentrate CO_2 close to the enzyme.

5.1. Photosynthetic bacteria: creating a CO_2 reservoir close to the RubisCO

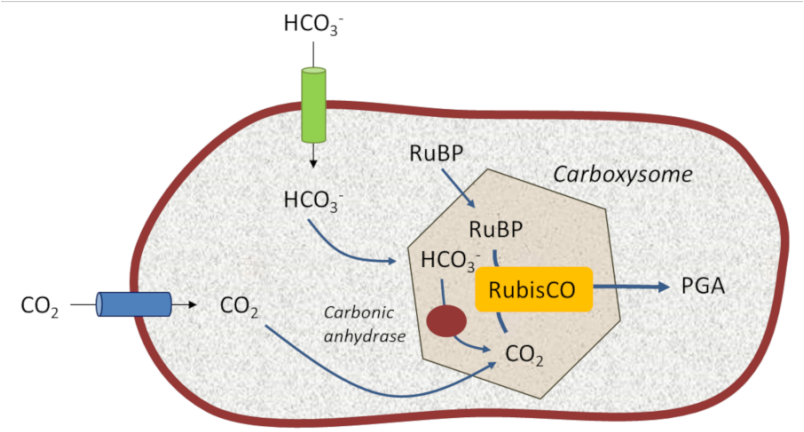

Figure 8. Carboxysomes are micro-compartments located inside the bacterial cell. [Source: © Jean-François Morot-Gaudry]

The photosynthetic machinery of photosynthetic bacteria is located in their cell membranes. Thus, **cyanobacteria** have in their cells micro-compartments, the **carboxysomes**, formed by a polyhedral protein shell, containing enzymes involved in carbon fixation (Figure 8).

These structures allow **cyanobacteria** to live in **aquatic environments that are poor in dissolved CO_2 but rich in bicarbonate HCO_3^- ions**. Specific and efficient transporters, located on their limiting membrane, capture bicarbonate (HCO_3^-) which they transform into CO_2 thanks to specific enzymes called carbonic anhydrases*. This **mechanism creates an internal reservoir of concentrated carbon dioxide** in the environment **close to their RubisCO**, thus somehow recreating the primitive atmosphere of ancient geological times. This promotes the carboxylase activity of RubisCO at the expense of the oxygenase activity. [13]

5.2. How to physically separating CO_2 fixation and RubisCO? the solution of C4 plants

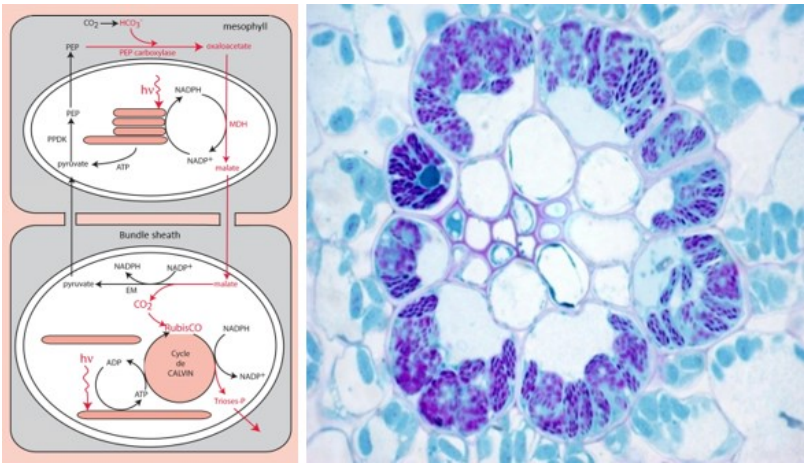

Figure 9. Diagram representing the juxtaposition -in two types of cells- of the C4 (mesophyll cells) and C3 (sheath cells) cycles in plants with C4 type metabolism (left). The C4 cycle enables CO2 to be concentrated in the vicinity of the RubisCO, thus promoting its carboxylase activity (Schéma Roger Prat, in Morot-Gaudry, Dunod, 2009). PGA, phosphoglyceric acid; RuBP, ribulose bisphosphate; PEP, phosphoenolpyruvate; HCO3-, bicarbonate. Right: Anatomy of a corn leaf section, a C4 plant. In light blue: chloroplasts of the mesophyll cells (C4); in blue-violet: chloroplasts of the perivascular sheath (C3). In the center, the cells of the conducting vessels. [Source: © Photo Frédéric Dubois, Université de Picardie]

Some plants, such as maize, have also developed an efficient mechanism for concentrating CO_2. Internal to the sheet, this mechanism involves two different tissues (Figure 9) :

One surrounding the conducting vessels, the outermost tissue, the mesophyll;

The other one surrounding the most internal tissue, the perivascular sheath (a very impervious russian nesting dolls type of structure).

Mesophyll cells contain specific **carboxylases**, phosphoenol-pyruvate-carboxylases or **PEP-carboxylases**, which catalyze the formation of a **four-carbon compound** (hence the name photosynthesis or C4-type plants), oxaloacetate [14] :

PEP (C3 molecule) + Bicarbonate (C1 molecule) → Oxaloacetate (C4 molecule)

In the mesophyll chloroplast, oxaloacetate is transformed into another C4 compound, malate, and migrates into the cells of the sheath. There, after enzymatic decarboxylation of this four-carbon compound, a significant amount of CO_2 accumulates in the environment close to the RubisCO, promoting its carboxylase activity. The phosphoenol-pyruvate is then regenerated to ensure the durability of the cycle.

This **mechanism** - which **physically separates** the **capture of atmospheric carbon dioxide** and its **use by the RubisCO -** has, however, an additional energy cost in ATP compared to the C3 mechanism of photosynthesis. [15]

5.3. Temporal separation in succulent plants: C4 metabolism at night and C3 during the day

In succulent plants (cacti, pineapples, etc.) or more generally plants with *the* CAM-type (Crassulacean acid) metabolism, the functions of CO_2 concentration and carboxylation of RubisCO are located in the same tissue. But there is a temporal separation of their functioning: at night C4 metabolism is active, ensuring malate synthesis, whereas during the day C3 metabolism is active owing to CO_2 released by malate decarboxylation. [16] (see Focus Joubarbe: example of a plant's adaptation to environmental constraints).

6. Photosynthesis in a changing environment

6.1. How metabolic types favor plants adaptation to environmental changes?

Figure 10. Corn field, a C4 plant. [Source: Lars Plougmann / CC BY-SA 2.0]

Temperature is a key environmental factor, and has different impact on C3 and C4 plants photosynthetic activity. For instance, above 30°C, C4 plants and CAM plants adapted to very dry regions are strongly favoured.

Under high illumination and high temperatures, C4 plants -showing virtually no photorespiratory activity- are more efficient at assimilating carbon from atmospheric CO_2 than C3 plants, provided that water and minerals are not limiting. For example, the 5% of C4 plant species on the planet fix 30% of the world's CO_2. And furthermore:

For the same biomass production, C4 plants use at least one third less water due to their sleeve leaf structure. Only 350 litres of water are needed to produce 1 kg of maize (a C4 plant, Figure 10) flour compared to 500 litres of water for 1 kg of wheat (a C3 plant, Figure 11) flour;

C4 plants mobilize less nitrogen than C3 plants because the efficiency of PEP-carboxylases allows to reduce the quantity of RubisCO -an enzyme very rich in nitrogen-, to reach the same photosynthetic activity as C3 plants.

Figure 11. Wheat field, a C3 plant, at sunset. [Source: Dreamy Pixel / CC BY 4.0]

In temperate regions, however, where light and temperature are lower, this difference in the photosynthetic capacity of C4 plants fades.

Moreover, if the concentration of CO_2 continues to rise in the atmosphere as it is currently observed (see A carbon cycle disrupted by human activities), C3 plants are expected to reach photosynthetic activities approaching those of C4 plants provided that temperatures remain moderate.

6.2. And in the future?

This observations suggests that, over the coming decades, plants will most likely acquire mechanisms for adaption to their changing environment.

Our better knowledge of the different mechanisms by which plants adapt to environmental changes allows us to consider developing plants that could be better adapted to rapid changes in CO_2 content, temperature rise, water availability, etc. Of the many research projects currently underway, it is not yet known which of them will prove to be profitable and suitable for large-scale agricultural or industrial application. The focus Improving photosynthesis? presents some possible directions.

7. Messages to remember

Through photosynthesis, plants and certain bacteria convert part of the sunlight into stable chemical energy and simultaneously fix the carbon dioxide CO_2, so as to elaborate all the organic molecules necessary for the development of life.

The use of radioactive ^{14}C as a molecular marker and the development of analytical techniques have made it possible to deciphering the carbon metabolic pathway and to highlight the Benson-Bassham-Calvin Cycle. This cycle ensures the regeneration of the carbon acceptor of CO_2 and the synthesis of the elementary molecules at the origin of sugars, proteins and lipids necessary for the elaboration and functioning of photosynthetic cells.

The carbon fixation of CO_2 which integrates the Benson-Bassham-Calvin Cycle has been catalyzed for several billion years by a specific enzyme of photosynthesis, ribulose bisphosphate carboxylase (RuBP carboxylase).

As a result of the increase in the planet's oxygen content (in the atmosphere and the oceans), the RuBP carboxylase has also fixed oxygen, thus manifesting not only a carboxylase function but also an oxygenase function, hence its name RubisCO.

The oxygenase function is responsible for the synthesis of a phospho-glycolate molecule, a powerful inhibitor of the Benson-Bassham-Calvin Cycle. Plants in the course of evolution have retained a metabolic pathway that eliminated 2P-glycolate with CO_2 emission, hence the name photorespiratory cycle.

Other photosynthetic organisms have developed more original and effective strategies by creating additional mechanisms, like the C4 cycle, which ensures a CO_2-rich environment around the RubisCO, more favourable to carboxylation and thus minimizing the oxygenase activity that inhibits photosynthesis.

Notes and References

We thank Editions Dunod and QUAE for having authorized us to reproduce figures for this article.

Cover image. [Source: Photo © Jean-François Morot-Gaudry]

[1] Carbon 11 (^{11}C) is an isotope of carbon with a half-life of 20.38 minutes. Experiments using this radioactive isotope must therefore be very short because it can no longer be detected after a few hours. It's commonly used to mark molecules in " *positron emission tomography* ».

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[4] Biology is based on the chemistry of carbon, because of its electrochemical potential, i.e. the part of chemistry that studies the reciprocal transformations of chemical energy and electrical energy. This very high potential proves capable of maintaining

four different chemical bonds at the same time, which makes it possible to multiply the various possibilities of atomic and molecular combinations, sources of the diversification of organic molecules essential to the various processes of evolution and development of life.

[5] Dalton is a standard unit of measurement, used to express the mass of atoms and molecules. Initially defined as 1/12 of the mass of a carbon 12 atom. The kilodalton (kDa) is much more used in biology and biochemistry because of the size of the molecules. Most cellular molecules typically have a mass between 20 and 100 kDa.

[6] Nitrogen is a major component of amino acids and proteins (about 6% of the mass of a protein).

[7] Otto Heinrich Warburg (1883-1970), German physician, physiologist and biochemist. Winner of the 1931 Nobel Prize in Physiology or Medicine "for his discovery of the nature and mode of action of the respiratory enzyme."

[8] Currently, the level of CO_2 in the atmosphere has exceeded 400 ppm (0.04%). Values above 415 ppm were recorded throughout 2019 at the Mauna Loa Observatory in Hawaii.

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