How do plants cope with alpine stress?

Auteurs :
STREB Peter, Maitre de conférences, Laboratoire d'Ecophysiologie végétale, Université Paris-Saclay
CORNIC Gabriel, Professeur honoraire, Laboratoire d'Ecophysiologie végétale, Université Paris-Saclay
BLIGNY Richard, Directeur de recherche retraité du CNRS, Laboratoire de Physiologie cellulaire et végétale, Université Grenoble Alpes

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At high altitudes, plants can be subjected to strong constraints: high light and UV radiation, low CO_2 concentration, large temperature variations… These parameters vary over the seasons but can also change significantly from one day to another as well as during the same day. These constraints modulate and sometimes disturb photosynthesis, which uses the energy provided by light and allows the growth and development of plants living in the alpine environment. In particular, excess light energy leads to the formation of toxic compounds, such as reactive oxygen species (ROS). To adapt to these difficult conditions, alpine plants developed various strategies: very small size, protective screen against UV radiation, protective anatomical structures, mechanisms to dissipate excess light energy, detoxification of reactive oxygen species, etc.

1. Vegetation in the alpine stages

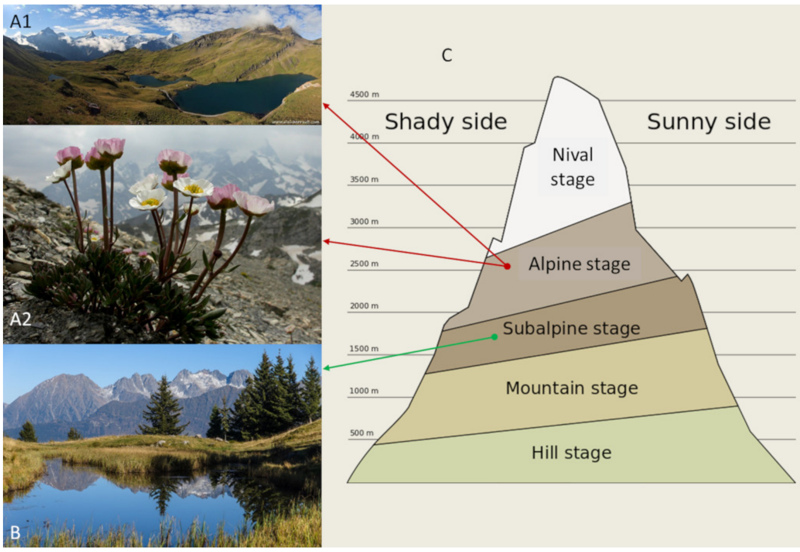

Figure 1. The various levels of vegetation in the mountains. The photographs represent the vegetation in the alpine and subalpine zones of the Northern Alps. The boundaries of the zones (or ecotone) vary with exposure: the sunniest face is generally the south face of a mountain, the least sunny face is the shady face, facing north. A1, alpine landscape; A2, Ranunculus glacialis, photo taken near the Galibier. B, landscape of the subalpine floor in the Belledonne massif. C, Theoretical representation of the various vegetation levels [Sources: A1, © Alain Herrault ; A2, © Serge Aubert, Station alpine Joseph Fourier; B, © Jacques Joyard; C, diagram by Pethrus (CC BY-SA 3.0) via Wikimedia Commons]

In mountains, the vegetation has characteristic zonations from valleys to peaks. In the Alps, deciduous forests are found in the lower parts, gradually replaced by conifers up to 1800-2300 m, depending on the exposure (sunny or shady side): it is the **subalpine stage** with an open forest and isolated trees in the upper part. Higher up, up to about 3000 m, the slopes are covered with lawns: this is the **alpine stage**. Beyond that, the alpine lawn gives way to a disjoint vegetation cover{ind-text}Characterizes an area of vegetation divided by rocks, screes, etc.{end-tooltip}, mosses and lichens, bare rocks and eternal snow: this is the **nival stage** [1],[2] (Figure 1). Plant biodiversity then declines sharply at high altitudes [3], with climatic factors seeming to be a barrier to the development of most plants.

2. Climatic conditions and the growing season

Figure 2. Plants under the snow. On the left, Soldanella alpina piercing the snow in spring. On the right, Ranunculus glacialis photographed after a snowfall in July. [Source: Photos © Peter Streb]

The average air temperature decreases by about 0.65°C every 100 m [1] (see The Earth's atmosphere and gaseous envelope). With increasing altitude, the precipitation is in the form of snow increases, which remained for a longer period, thus limiting the vegetation period{ind-text}The period when a plant grows, develops and reproduces. This period is in contrast to the slower life phases in the form of seed, spore, underground organ, or defoliated tree{end-tooltip} [2]. At high altitudes, plants are most often "perennial": they survive for several years [3]. Annual plants germinate, form roots, stems, leaves and flowers, every year and produces new seeds during a short growing season (see Reproductive strategies of alpine plants). On the other hand, perennial plants enter dormancy in winter and keep reserves in the roots, bulbs, tubers and rhizomes{ind-text} Underground stem that carries leaf and root buds. A rhizome can be horizontal and more or less close to the surface, such as the iris, or much deeper, such as the bindweed.{end-tooltip}. In some species, the stems and leaves remain alive, which allows them to restart quickly in spring, as soon as the ground is free of snow.

Thus, perennial plants have the advantage of neo-forming only a few organs during the growing season whereas annual plants must form all their organs, which consumes a lot of energy for a limited time.

Figure 3. Silene acaulis, an example of an alpine cushion plant that resists very low temperatures. [Source: Photo © Peter Streb]

On the other hand, the survival organs of perennial plants must tolerate low winter temperatures. Freezing temperature has often been measured in alpine plants. They change during the year, falling to its lowest level during winter [3],[4]. For example, during this period, the green leaves of *Soldanella alpina* (Figure 2) resist -20°C, while those of *Carex firma* and *Silene acaulis* (Figure 3) withstand more extreme temperatures: -70°C and -196°C respectively [4]. It is likely that these low freezing temperatures can help alpine plants in the event of particularly severe episodes, outside the snow cover. Indeed, the temperature under the snow is always higher than in the open air [4]. Thus, it is likely that the ability to withstand very low temperatures is not likely to limit the distribution of plants at high altitudes.

3. Photosynthesis

During the growing season, plants ensure their **growth** and **development** through **photosynthesis**. In this process, the necessary energy is provided by solar radiation, which allows the synthesis of organic matter from carbon dioxide taken from the atmosphere, and water and minerals taken from the soil. Because photosynthesis is affected by multiple environmental constraints such as those present at high altitude [5], it is likely that the maintenance of photosynthesis under stress conditions determines the survival of plants at high altitude. The main reactions of photosynthesis are summarized in Figure 4 and detailed in [6]. Figure 4 also describes the particularities implemented by alpine plants to protect this process.

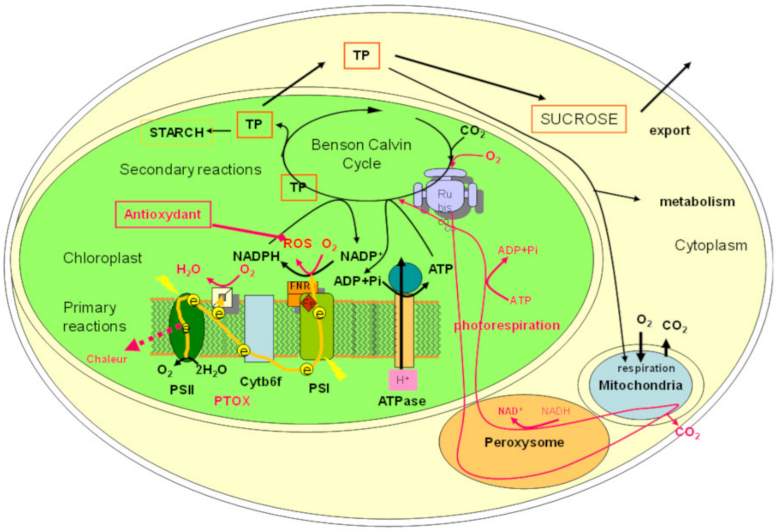

Figure 4. Schematic representation of a chlorophyll-containing cell showing some aspects of the cooperation between chloroplast, cytoplasm (with mitochondria and peroxysomes), and the main protein complexes involved in photosynthesis. Light absorption and electron transport in the primary reaction of photosynthesis, related to the thylakoid membrane, are shown in yellow. This reaction includes the protein complexes PSII, Cytb6f, PSI and ATPase. The black arrows show the use of energy for CO2 assimilation in the secondary reaction and for sugar synthesis as well as their use in the cell. There are also alternative ways of using absorbed energy (shown in red), whose functioning can protect photosynthesis: the emission of excess energy in the form of heat, the reduction of oxygen in water by the PTOX protein, the formation of ROS by the PSI and their detoxification by antioxidants, finally the photorespiration path initiated by the absorption of oxygen by Rubisco. For details see the text. Diagram © Peter Streb. Abbreviations ; AT(D)P: Adenosine tri(di)phosphate; Cytb6/f: cytochrome b6/f; e: electron - electron transport between PSII and NADP+ is indicated; Fe: Ferredoxine; FNR: Ferredoxine-NADP-Reductase; NADP(+H : Nicotinamide adenosine di-nucléotide phosphate (+ oxidized form, H reduced form); PSI & PSII: photosystem I and II; PTOX: plastic terminal oxidase; Rubisco: ribulose-bis-phosphate carboxylase oxygenase (enzyme complex that catalyzes CO2 fixation); SDP: sucrose-di-phosphate (substrate for Rubisco); TP: triose phosphate (first phosphorylated sugar appearing after CO2 assimilation).

Photosynthesis takes place in the chloroplasts{ind-text}Organites of the cytoplasm of photosynthetic eukaryotic cells (plants, algae). As a site of photosynthesis, chloroplasts produce O_2 oxygen and play an essential role in the carbon cycle. They use light energy to fix CO_2 and synthesize organic matter. They are thus responsible for the autotrophy of plants. Chloroplasts are the result of the endosymbiosis of a photosynthetic prokaryote (cyanobacterium type) within a eukaryotic cell, about 1.5 billion years ago.{end-tooltip} and can be divided into two phases.

A primary phase takes place in the membrane of the thylakoids: the solar energy is absorbed by **photosynthetic pigments (chlorophylls** forming collecting antennas), then transferred to two **reaction centres** (photosystem I and II: PSI and PSII) whose coordinated activity results, *via* a succession of **redox reactions**, in the reduction of NADP+ to NADPH{ind-text}Sigle for the reduced form of the coenzyme Nicotinamide Adenine Dinucleotide Phosphate (NADP). NADP is formed from Nicotinamide Adenine Dinucleotide (or NAD) by binding a phosphate to the 2' hydroxyl group of the ribose associated with adenine. It exists in an oxidized form, called $NADP^+$, and a reduced form, called NADPH. The NADPH is said to carry reductive power: used in catalyses carried out by oxidoreductases, it is capable of supplying energy during the transfer of their hydrogen atom, allowing the reduction reactions necessary for cellular functioning.{end-tooltip} by the PSI. The electrons involved come from the oxidation of water ($2H_2O \rightarrow O_2 + 4H^+ + 4e^-$) at the PSII level. This primary phase also induces the establishment of a proton gradient on the thylakoid membrane which provides the energy necessary for the synthesis of ATP{ind-text}Abbreviation of adenosine triphosphate. A triphosphate nucleoside composed of adenine (nitrogen base), ribose (sugar with 5 carbon atoms) and three phosphate groups forming a triphosphate group. A compound that both donates and stores energy present in all living organisms. Also used as building materials for nucleic acid synthesis.{end-tooltip} (Figure 4).

The second phase of photosynthesis takes place in the chloroplast stroma. It consumes the ATP and NADPH formed to fix atmospheric CO_2 on a sugar di-phosphate (activity of RuBisCO{ind-text}Abbreviation for ribulose-1,5-bisphosphate carboxylase/oxygenase. It is the key enzyme for fixing CO_2 carbon dioxide in plant biomass by initiating the Benson & Calvin cycle, using solar energy captured by chlorophyll during the photosynthesis process.{end-tooltip}), whose skeleton is formed by 5 carbon atoms (Ribulose bisphosphate or RuBP) and give sugar-phosphates with three carbon atoms (Triose-phosphate, in short TP) (Figure 4). This type of photosynthesis, which quickly leads to the formation of compounds with 3 carbons, is characteristic of C3 plants (C3 for 3 three carbons). The latter constitute the vast majority of alpine plants.

Trioses phosphate (TP), which contain assimilated CO_2, can be used in chlorophyll-containg cells in several ways: (1) to regenerate the CO_2 acceptor; (2) for the synthesis of **glucose** and **starch** in the chloroplast; (3) to be exported to other compartments of the cell where they provide energy and carbon chains for its maintenance; (4) for the synthesis of sucrose which is exported to other parts of the plant as an energy source and supplier of carbon skeletons feeding numerous biosyntheses [6]. Note also that oxygen can bind to RuBP: this oxygenation is at the origin of a metabolic pathway, photorespiration, which also consumes ATP and NADPH (Figure 4).

4. Importance of environmental factors in photosynthesis

4.1. Temperature

During photosynthesis, temperature mainly affects reactions allowing the binding of CO_2 and O_2 and the synthesis of sugars, but also the exchange of molecules between cellular compartments. The two main phases of photosynthesis and the transport processes involved are affected differently by **temperature**:

Biophysical processes such as light absorption by chlorophyll pigments and the formation of NADPH and ATP are not or only slightly temperature dependent.

The biochemical reactions of CO_2 and O_2 assimilation and sugar synthesis, as well as the exchange of molecules between cell compartments, are highly temperature dependent [7]. On average, a 10°C increase doubles the rate of **biochemical reactions** [6].

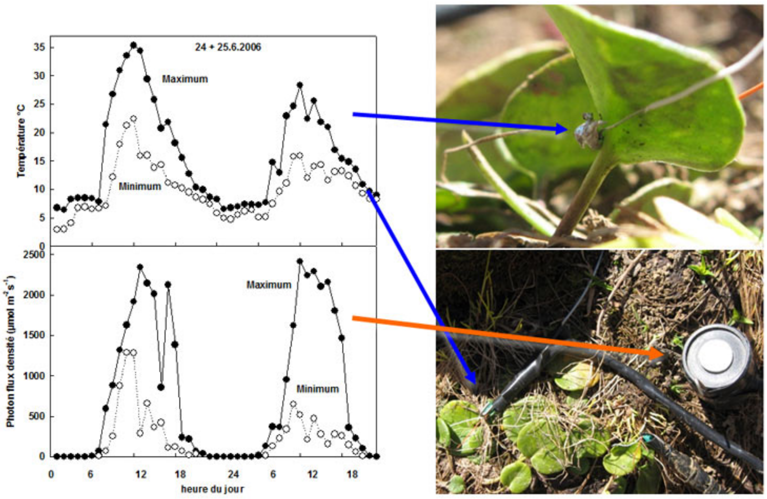

Figure 5. Measurement of temperature and light intensity in alpine plants. Graphs on the left: Temperature & light intensity (expressed as photon flux density) measured at 2400 m in the Lautaret Pass area on the surface of a Soldanella alpina leaf. Maximum and minimum values are shown on the graph. The amplitude of the greatest thermal variation is 32°C between night and day and 15°C during the same hour. The photon flux density can vary from 2000 µmol $m^{-2}s^{-1}$ over the course of an hour. Right: photos of Soldanella alpina showing the installation of temperature and light sensors [Source: Diagram © Peter Streb and Constance Laureau, unpublished; Photos © Constance Laureau]

During the growing season, the temperature of the leaves of alpine plants can vary by 30°C between night and day, and by 15°C during the same time of day (Figure 5). Thus, the rate of biochemical reactions can vary by a factor of 8 between night and day and 3 during the same hour in a leaf. In summary: at certain temperatures, the light energy captured by the leaf is not entirely consumed by biochemical reactions.

For example, the glacier buttercup, under light providing 2000 µmol photons $m^{-2}s^{-1}$, fixes about 15 µmol CO_2 $m^{-2}s^{-1}$ at 23°C (see Figure 5 for the order of magnitude of the luminous flux), and only fixes half of it when it is at 10°C. In the first case the light is not saturated and the fixation of CO_2 can eliminate the energy it provides, in the second case, however, the fixation of CO_2 is already saturated under 500 µmol photons m^{-2} s^{-1} and therefore the light is largely excess [8].

4.2. Light

Like temperature, light can change suddenly by several orders of magnitude during the same day in alpine conditions (Figure 5).

Under cloudy sky, the average light intensity is not very different between valleys and high altitude [3]. On the other hand, the maximum light intensity in clear weather is much higher at high altitude, exceeding the photosynthetic capacity of most plants. Just like a drop in temperature, very strong light causes an excess of energy in the leaves that can damage photosystems [7]. In addition, there is more ultraviolet radiation (UVA and UVB) at higher altitudes [9], which can directly impact cellular structures: photosystems, but also DNA in the chloroplast, mitochondria and nucleus (see Cellular impact of solar UV). At the PSII level, manganese, which is involved in oxygen production (Figure 4), and plastoquinone, which transports electrons between the PSII and cytochrome b_6/f ($cytb_6f$), directly absorb UV radiations and in this way their function can be blocked [10].

A shade plant takes advantage of the moderate light intensities, which are common in the Alps, but is stressed if the light intensity is too high. On the other hand, a sun plant is more tolerant to high light intensities, but does not use weak light as well [11]. Finally, bright alpine plants such as *Soldanella alpina*, *Homogyne alpina* or *Ranunculus glacialis* (Figure 2) do not show any typical specific adaptation to low or high light [11].

4.3. Other factors

Other alpine environmental factors affect photosynthetic activity:

The decrease in **air pressure** at high altitudes, for example, reduces the availability of CO_2 [7].

The **wind** - whose strength depends on the topography - increases the risk of plants drying out.

By promoting rustle, the slope also reduces **water retention by the soil** [3].

However, in case of water stress, a plant reacts by closing its stomata (specialized cells controlling the gas exchange of the leaf): this limits the supply of CO_2 and slows down photosynthesis. Here again, the biochemical reactions of photosynthesis cannot consume the excess light energy received by the plant.

In summary, climatic factors (such as light, temperature, humidity) vary strongly, rapidly and with large amplitudes in the mountains. If the majority of lowland plants are exposed to such variations, they do not survive, because photosynthesis is not able to use the excess energy [7]. This excess energy can be transferred to oxygen by forming reactive molecular oxygen species (ROS) (Figure 4 and [12]). ROS are potentially very destructive molecules; they can damage not only the photosynthetic apparatus and particularly photosystem II (photoinhibition{ind-text}A process by which excess light decreases the speed of photosynthesis in organisms capable of performing it.{end-tooltip}), but also the entire cell (seeThe fixed life of plants and its constraints). In the end, the plant's photosynthetic capacity may be inhibited by ROS, and its ability to repair damage is greatly reduced [11].

4.4. What are the constraints for photosynthesis of alpine plants?

The constraints imposed by the alpine environment can be illustrated, for example, in two extreme cases.

Some alpine plants such as *Soldanella alpina*, *Geum montanum* and *Homogyne alpina* keep some green leaves during the winter. Photosynthesis of these leaves begins immediately after snowmelt, under conditions that combine high light intensities with high thermal gradients [7]. These alpine species must take advantage of the short period after snowmelt for their photosynthesis, because they will be shaded by the other plants a few weeks later. Inactivation of photosynthesis in extreme climates can be lethal to these plants.

However, most alpine plants do not keep their leaves in winter and must quickly mobilize their reserves to form their first leaves and ensure their development cycle for a short favourable period. The case of *Ranunculus glacialis* (see Figure 2), which is only found above 2200 m, shows that this can be even more complex. Indeed, in this plant, it is calculated that the reserves mobilized for leaf formation represent about 30 days of photosynthesis, which can hardly be achieved during the growing season [3]. As *Ranunculus glacialis* flowers need two years to mature [12], this suggests that the energy received during a single growing season is not sufficient to complete its development cycle in one year. *Ranunculus glacialis* cannot therefore risk inactivation of photosynthesis. Dwarfing of several alpine species can also be considered as a strategy limiting the investment of energy in the formation of photosynthetic tissues.

5. Acclimation in alpine plants

Acclimation involves responses to minimize the amplitude of variations in the physical parameters of the environment at the plant level, before they exert their negative effects at the cellular and molecular level. When these responses are insufficient, acclimation is manifested through other protections to prevent the destruction of cells or their organelles.

Alpine plants often have a particular architecture in pillows (see Figure 3), rosettes or tussocks (see Inheritance or convergence). This type of morphology puts the plants in a favourable microclimate [3] with: (1) a decrease in light intensity and UV radiation aborbed by leaf tissue; (2) an increase in moisture at the level of leaves with wind protection, limiting drying out; (3) lower temperature variations than in the surrounding air. The acquisition of this type of morphology represents a first avoidance response. Of course, the growth of these plants is much slower than that of the plants that do not form these structures: this is the price to pay.

As described above, very large thermal variations combined with high luminosity can induce photoinhibition of photosystem II and the formation of ROS.

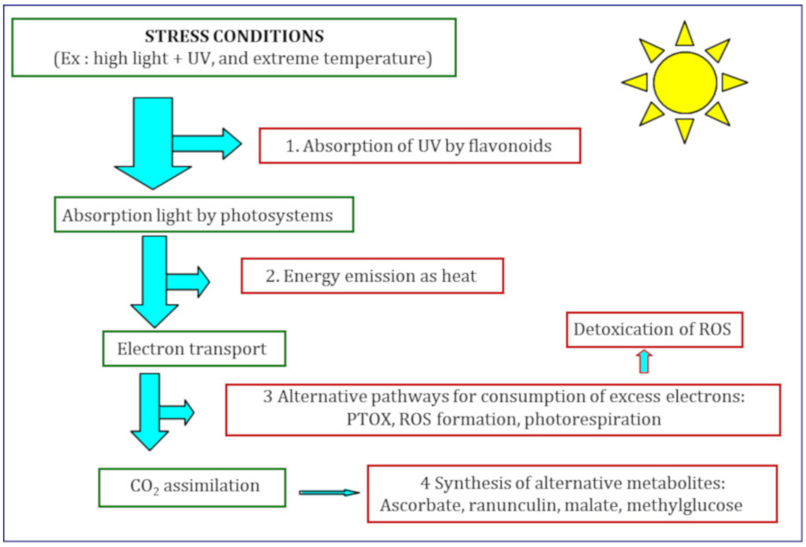

Figure 6. Energy flow in the leaf under stress and light conditions and protective mechanisms in alpine plants. (1) Some of the radiation is absorbed in the epidermis by flavonoids, particularly UV radiation. (2) Some of the energy absorbed by the photosystems can be emitted as heat. (3) Some excess electrons may be transferred to oxygen to form water by PTOX, or ROS or consumed by photorespiration. ROS can be detoxified by the antioxidant system. (4) Synthesis of some sugars and metabolites characteristic of alpine plants. For details see also Figure 4. [Source: Diagram by Peter Streb]

Compared to lowland plants, the alpine plants we studied [7] are much more resistant to photoinhibition. To achieve this, they use different protection mechanisms, most of which also exist in lowland plants. These are avoidance mechanisms that occur at several organizational levels (for details of several protection mechanisms see Figure 4). They can be divided into two categories. "Upstream" mechanisms that avoid the too rapid arrival of energy on the reaction centres and "downstream" mechanisms that maintain the use of the electrons separated in photosynthetic reactions (*i.e.* ultimately the use of the light energy captured by the antennas) even under adverse conditions (see Figure 6).

Protection against UV radiation. At the epidermal level, some species synthesize flavonoids{ind-text} Secondary metabolites of plants, all sharing the same basic structure. With several thousand compounds, flavonoids are the most important category of polyphenols and represent a gigantic family of antioxidants. Flavonoids are responsible for the brown, red and blue tones of flowers and fruits.{end-tooltip}, pigments that absorb high-energy UV radiation. Thus, UV does not excite the underlying cells. This flavonoid screen thus protects the photosystems and prevents the destruction of the DNA of chlorophyll-containing parenchymes{ind-text}Tissues composed of chlorophyll cells containing many chloroplasts. As the site of photosynthesis, they participate in nutritional functions. They represent an important part of the inside of the leaves. {end-tooltip}. In *Soldanella alpina*, for example, protection by high flavonoid contents is induced by strong light and increases with altitude [13].

Re-emission of the excess energy absorbed. Light collecting antennas change conformation in illuminated plants; at the same time, some of the excited chlorophylls pass their energy to carotenoids (zeaxanthin for example). This allows some of the light energy to be dissipated as heat (Figure 4). In this way, the amount of energy arriving at the reaction centres is controlled. Under excess light, the thermally dissipated light fraction is higher than that directed towards the reaction centres. Thermal dissipation is a quick way to remove the excited states of chlorophyll. However, while in some alpine species, such as *Soldanella alpina* and *Geum montanum,* this avoidance mechanism is very effective, in others, such as *Ranunculus glacialis*, it is not very effective and other mechanisms are activated (see below) [7].

Energy transfer to alternative acceptors via an electron flow. In chloroplast, the alternative oxidase (called

PTOX{ind-text}Enzyme of the membranes of the chloroplast thylacoids, which catalyzes the oxidation of the plastoquinone pool, hence its name alternative oxidase (PTOX).{end-tooltip}), connected between the two photosystems (Figure 4), accepts electrons provided by the PSII and transfers them to molecular oxygen, thus creating water. This enzyme can thus reduce electronic pressure and thus the formation of ROS under excess light. Compared to lowland plants, the content of PTOX in alpine plants is high and its concentration increases with altitude in *Geum montanum* [7],[8].

Maintaining photosynthetic metabolism at low temperatures. If the CO_2 supply limits the synthesis of sugars in the second phase of photosynthesis, Rubisco catalyzes the binding of molecular oxygen to RuBP. This is the first step in photorespiration (Figure 4). Photorespiration consumes energy, in the form of (a) carbon (RuBP), (b) electrons produced during the first phase of photosynthesis and (c) ATP. The activity of photorespiration, usually negligible at low temperatures, becomes important when the latter exceeds 20°C. In *Ranunculus glacialis*, which does not tolerate heat, photorespiration is already active when the temperature is low [7],[8].

Synthesis of specific metabolites. Some alpine plants synthesize metabolites that are generally absent or present in small quantities in lowland plants. The function of these metabolites is often not understood. But their synthesis consumes part of the energy captured by the photosynthetic apparatus and can thus help to protect it. Thus, *Ranunculus glacialis* accumulates significant amounts of ranunculin{ind-text}Glucoside produced by plants such as ranunculus (Ranunculaceae). A highly unstable molecule, it is hydrolyzed into an irritating lactone: proto-anemonin {end-tooltip} and malate{ind-text}Malic acid salt, a dicarboxylic acid widely used in the plant kingdom and naturally present in fruit, which contributes to its pleasant taste. Malate is an intermediate of the Krebs cycle, one of the major metabolic pathways of cellular respiration in almost all living beings, and is involved in the Benson & Calvin cycle, which is part of photosynthesis. Used as a food additive, under number E296 {end-tooltip} [14]. *Geum montanum* contains high concentrations of methylglucose{ind-text}Monosaccharide (glucose) with a methyl group (CH_3).{end-tooltip}, while *Soldanella alpina* contains record amounts of ascorbate (vitamin C) in its leaves [15]. Ascorbate is part of the antioxidant system that protects the plant from ROS.

Detoxification of highly reactive forms of oxygen (ROS). Environmental constraints increase the formation of ROS, especially during the early stages of photosynthesis. In Figure 4, ROS formation is indicated at the PSI level: it is the major pathway for the formation of ROS in light. To degrade ROS to oxygen, plants use a set of enzymatic reactions with associated metabolites. In *Soldanella alpina* leaves, the antioxidant system is based on the presence of vitamin C and vitamin E, as well as enzymes involved in redox processes [7]. In *Potentilla saundersiana*, the importance of the antioxidant system of the leaves increases with altitude [16].

In short, it is a set of protection mechanisms that allow alpine plants not only to survive, but also to develop in a habitat that becomes more and more restrictive with altitude. These mechanisms complement and add up to facilitate the life of alpine plants (Figure 6).

References and notes

Cover image. Alpine *linaria (Linaria alpina)* in the Galibier schists (2600 m). [Source: Photo © Serge Aubert/SAJF]

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