

The fixed life of plants and its constraints

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05-12-2019



Plants are fixed to the soil by their roots, which supply them with water and minerals, their leaves capturing solar energy to fix the carbon from carbon dioxide. These essential processes of earthly life are therefore carried out by immobile organisms. Plants must therefore be able to adapt to the contrasting and fluctuating conditions of their environment, without the possibility of finding a more favourable habitat than movement would allow them, as is the case with animals. Evolutionary forces have helped to shape the development and physiology of plants to adapt to the different climatic zones of the planet, from taiga to desert, through tropical or temperate zones. The resulting plant biodiversity is of enormous richness. But environmental variations in the same place on our planet

can also fluctuate greatly with the seasons. Plants of the same species then acquired cellular and molecular mechanisms allowing them to perceive external changes and reprogram the expression of their genome. They can thus redirect their development, physiology and metabolism in order to adapt as effectively as possible to these changes

1. Plants: sessile organisms that adapt without moving

The word adaptation comes from the Latin *adaptare*. It can be defined as a set of adjustments or changes in the behaviour, physiology or structure of an organism that enable it to become better able to live in a defined environment.



Figure 1. Plant vitality: bare soil ploughed in the fall will regrow in the spring! [Source: Banque d'images pédagogiques des Vosges (see ref. [11])]

From this point of view, plants are remarkable because they are adapted to their environments. They are so integrated into our daily lives that we sometimes forget them! They are simply there... immutable! Just look at a ploughed field in winter, where only the soil is visible, and revisit it in spring, covered with such a familiar green, to become aware of the extraordinary vitality of plants (Figure 1, [11]).

Whether it is windy, rainy, snowy, freezing to death or that a scorching heat wave overwhelms us... the plants are there! It is indeed one of their characteristics to adapt to highly fluctuating environmental conditions. Plants have to deal with very large **differences in temperature, light and humidity** depending on the time of day, the seasons and the places where they grow. The **nature of the soil** also determines particular conditions for plant growth and development, and significant **deficiencies** in mineral nutrients (nitrogen, phosphorus, etc.) may exist in the soil, or, in contrast, harmful **toxicities** due to excess toxic metals (cadmium, lead, aluminium, etc.) may occur. Some irrigation water, or land by the sea, causes saline stress {ind-text}Stress caused by soil salinity. This salinity can be natural or induced by agricultural activities such as irrigation (with low quality water) or the use of certain types of fertilizers. {end-tooltip} disrupting normal plant nutrition processes. These fluctuations in the physical environment favour the geographical distribution of plants according to their ability to adapt to a biotope {ind-text}Location with relatively uniform determined physical and chemical characteristics. This environment is home to a set of life forms that make up biocenosis: flora, fauna, micro-organisms. A biotope and the biocenosis it supports form a given ecosystem. There are **shade plants** such as ferns, which prefer to grow out of the light, or **aquatic plants** such as the élodée, which require a lot of water. Similarly, **calcareous soil** will support **calcareous plants** "that settle in limestone". This is the case for garrigue plants in the south of France. Plants that "flee from limestone" or **calcifuges**, such as chestnut trees or ferns, prefer **acidic soils**. But plants do not only interact with their physical environment. They also interact with other living organisms. Some may be **useful** to them by promoting their nutrition, for example, **symbiotic bacteria** and **fungi** mycorrhizal fungi {ind-text}Mycorrhizal relatives, which are symbiotic associations between the roots of plants and soil fungi. Mycorrhizae affect more than 95% of terrestrial plants. They give plants better access to soil nutrients and help them better resist environmental stresses. {end-tooltip}. Others are **harmful** to them by infecting them, such as **viruses, bacteria, phytopathogenic fungi**, or by eating them, as is the case with many insects and herbivores in general. Just as plants have adapted to the physical variations of their environment, they have, over the course of evolution, developed responses to defend themselves against the aggression of pathogens.

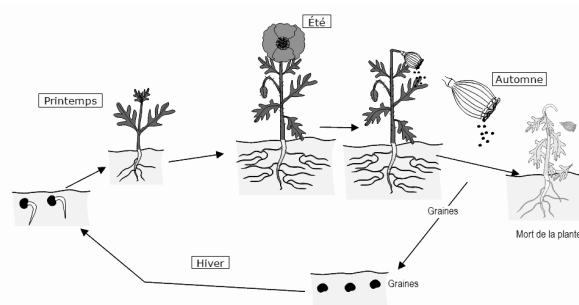


Figure 2. The life cycle of plants: in spring when temperature, humidity and light conditions are favourable, the seeds in the soil germinate and the roots and leaves of young seedlings allow the plants to develop. At a given stage of their development they flower and produce new seeds that will be buried in the ground to germinate the following year. Vegetative organs (roots, leaves) die in autumn when conditions become unfavourable... but if the individual plant has disappeared, the species persists thanks to the seeds. [Source: © Alain Gallien, Banque de Schémas, Académie de Dijon]

Plants are characterized by different states, vegetative (leaves, roots) or reproductive (seeds), and by their life cycle (Figure 2). There are **annual plants** that disappear in winter when conditions (light, humidity, temperature) are unfavourable to reappear the following spring from the germination of their seeds, or from underground storage organs such as bulbs and tubers. **Perennials**, on the other hand, are still clearly visible in the bad season, during which they often enter dormancy, losing their

leaves, such as **deciduous trees**, to resume growth in good weather, from their buds [2].

Unlike animals, plants do not flee to avoid adverse or aggressive conditions that jeopardize their integrity or survival. They do not have the central nervous system that allows animals to analyze the information their senses provide them, triggering actions to adapt to changing situations. They are fixed to the soil by their **roots**, which provide the aerial parts with water and essential mineral elements: nitrogen, phosphorus, potassium, sulphur, iron, zinc, magnesium, manganese... [3]. **Leaves** are able to transform the **light energy** provided by the sun into carbonaceous organic molecules (sugars, lipids, proteins) through the reaction of photosynthesis. Bioenergetic process that allows plants, algae and certain bacteria to synthesize organic matter from the CO₂ in the atmosphere using sunlight. Solar energy is used to oxidize water and reduce carbon dioxide in order to synthesize organic substances (carbohydrates). The oxidation of water leads to the formation of O₂ oxygen found in the atmosphere. Photosynthesis is at the base of autotrophy, it is the result of the integrated functioning of the chloroplast within the cell. [4] (link to article *Light on photosynthesis*). Briefly, let us recall that photosynthesis occurs in leaf specific cellular organelles. Specialized structures with a specific function within the cell. For example, the nucleus, mitochondria and chloroplasts, the chloroplasts. Organites of the cytoplasm of photosynthetic eukaryotic cells (plants, algae). As a site of photosynthesis, chloroplasts produce O₂ oxygen and play an essential role in the carbon cycle: they use light energy to fix CO₂ 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. Their **chlorophyll** captures solar photons leading to the cleavage of **water** molecules and the release of **oxygen**, the **assimilation of carbon** from carbon dioxide (CO₂) into organic molecules, and the **production of chemical energy** (Adenosine Triphosphate or ATP). 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}).

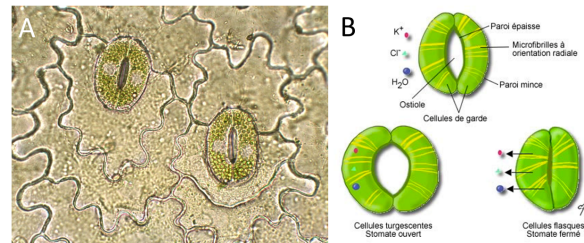


Figure 3. The stomata of the leaves. A, Two specific cells of the epidermis of the leaves, the guard cells, assemble to form a stomata; [Source: photo © Christophe Charillon ; cf. ref. 5]. B, Their bean shape defines an empty space in the middle, the ostiola, through which gas and water exchanges can occur between the leaf and the outer environment. The more or less important turgidity of the guard cells means that the ostiola can be opened or closed. Closing the stomata during the day when it is hot prevents the plant from losing its water. The closure of stomata is controlled by flows of ions (potassium, chloride, etc.) and water to neighbouring cells [Source: © Chantal Proulx; see ref. 6]

Gas exchanges (water vapour, oxygen and carbon dioxide) between plant leaves and the external environment are therefore essential. From an anatomical point of view, these exchanges occur in very specific leaf structures: **stomata** (Figure 3; [5],[6]) which are composed of two cells of the epidermis, called **guard cells**. Depending on the state of turgescence. A cellular state associated with the elongation of the plant or animal cell whose vacuoles or vesicles are expanding due to water entry into the same cell. of these cells, **stomata open and close** to allow these exchanges, depending on environmental parameters such as temperature, brightness or humidity [7]. Stomatal function and photosynthesis are therefore two important parameters that contribute to the adaptation of plants to their environment, especially for **drought adaptation** or for plants living in arid environments such as **deserts**, as we will discuss later in this article.

Plants, because of their fixed life and their lack of sensory organs for perceiving the outside world on the one hand, and of a central nervous system on the other, have therefore evolved to adapt to contrasting environmental conditions in space and fluctuating over time.

These two aspects of plant adaptation do not use the same concepts and mechanisms. In the first case, it is the spatial adaptation of different plant species to the different climates of the planet. Not all plant species grow everywhere, and this climato-geographical adaptation has been based on the principles of natural selection of beneficial traits, traits that have become established over time in the genetic heritage of the species (see [The adaptation of organisms to their environment](#)). The second case involves the adaptation of plants of the same species to fluctuating environmental conditions in a given place. A plant can thus successively undergo periods of drought, cold, high light intensity, etc. It adapts to these variations by activating physiological processes, often using reprogramming of gene expression leading to high phenotypic plasticity. The ability of an organism to express different phenotypes from a given genotype under environmental conditions. (see

It is therefore the combination of characteristics fixed in the genome of the different plant species and the plasticity of their genome expression that allows plants to cope, without moving, with very diverse environmental conditions.

2. Spatial adaptation of plants: from desert to taiga

Plants can be found all over the world, at all latitudes and longitudes, and at all altitudes. However, the conditions of temperature, luminosity and hygrometry are extremely variable in different climates. As dry as deserts are, tropical forests are full of water! It is enough to observe the plants that grow in these extreme environments to realize that they often do not belong to the same species and that they have morphological and anatomical characteristics very characteristic of the environment in which they grow [8].

Let us take two examples of radically different landscapes: the taiga{ind-text}Forest-type plant formation traversed by a vast lake system resulting from fluvioglacial erosion. Strongly linked to the subarctic climate, it is one of the main terrestrial biomes. It is a transition zone between the boreal forest and the Arctic tundra, Siberian{end-tooltip} and the Arizona desert (Figure 4).

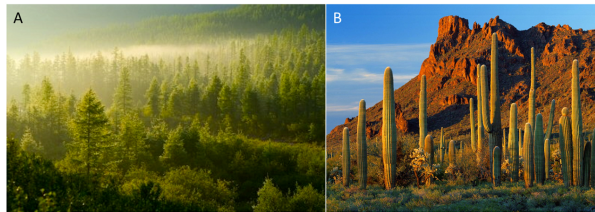


Figure 4. Vegetation diversity according to geography and climate. A, Conifers (fir, spruce,...) populate the Siberian taiga, [source: © Eniscuola.com] B, The Arizona desert is the land of the Saguaro, and more generally succulent plants, [source: © Derek Ostrovski].

Taiga is a transition zone between the boreal forest{ind-text}Forest dominated by conifers with discrete hardwood presence. In Europe, made up of deciduous (birch) and/or coniferous trees, it extends from the Baltic to the Urals. In Canada, it is the largest area of vegetation, accounting for 55% of the country's land area. {end-tooltip} and the arctic tundra{ind-text}Discontinuous plant formation in cold climate regions, including some grasses, mosses and lichens, and even some dwarf trees (birches). The tundra is characterized by a **ground perpetually frozen at depth** (permafrost). It covers the far north of the Northern Hemisphere, before bare ground and ice, between 55° and 80° latitude.{end-tooltip}. The forest cover is continuous but relatively open, composed of bushes, conifers and birches. The taiga is subject to a subarctic climate characterized by short, cool summers with prolonged periods of sunshine and very cold winters. The average temperatures of the warmest month are between 10 and 15°C, but the minimum winter averages can drop below -30°C. Rainfall is generally less than 500 millimetres per year.

A **desert** is a **very dry region** of the globe, characterized by rainfall of less than 200 and often even 100 mm/year, marked by poor soils and scarce plant populations. This lack of water is associated with irregular rainfall from one year to the next. Deserts are found at all latitudes and longitudes and cover about a third of the land surface, almost 100 times the size of France. They spread mainly across the Tropic of Cancer, in Western Asia, in the interior of Australia, and at polar latitudes. The common feature of all deserts is the lack of water. The low relative humidity of the air (generally less than 50%) and the clear sky most often explain the high temperature variations. In hot deserts, temperatures above 50°C during the day are followed by temperatures below 0°C at night.

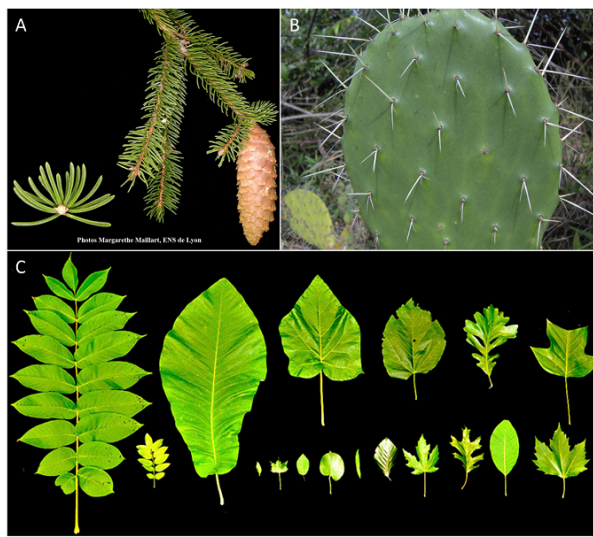


Figure 5. Diversity of leaf shape and physiology according to their adaptation to a climate and a geographical area. A, Taiga conifers have leaf needles that do not fall in the fall and have a reduced surface area for exchange with the outside world [source: © Margarethe Maillard, ENS Lyon]. B, Cactus leaves are even smaller and can be summarized as thorns to reduce water losses [source: © Siquisai (CC-BY-SA-3.0) via Wikimedia Commons]; C, Diversity of the shape of deciduous leaves of trees living in our temperate regions [source: © Kaare Jensen (Harvard University), Maciej Zwieniecki (UC Davis)].

The most common plants found in the **taiga** are **coniferous** trees: pines, firs, spruces. The main characteristic of most conifers is that they are **always green**, as they do not lose their leaves (Figure 5) when temperatures drop. This feature is an important adaptation because trees do not need to rebuild leaves in the spring, which requires a lot of energy. Taiga soils are often poor in nutrients, and the sun is generally low on the horizon. These two factors limit the amount of energy available to trees, and the fact that they are always green allows them to use this energy for growth rather than for leaf production. In addition, despite heavy rainfall, the ground freezes for many months (read [The permafrost](#)), preventing the roots from drawing water. Having needles rather than larger surface leaves allows conifers to limit water loss through transpiration. On the other hand, the needles contain little sap, limiting the risk of freezing. Finally, the particular habit of conifers is a remarkable adaptation to avoid the accumulation of snow on the branches that it might break.

In **deserts**, no coniferous trees! The flora is very particular (Figure 4), and perfectly adapted to **arid** conditions where water is the most precious commodity. This is the territory of succulent plants (fat plants, for example) adapted to survive in arid environments due to the characteristics of the soil and climate. such as **cactus**, which have reduced their leaf area to a minimum, sometimes to simple thorns, with stems providing photosynthesis activity (Figure 5). Plants living in deserts do so through three main modes of adaptation: succulence, tolerance to drought or drought avoidance. The so-called succulent plants, which include all species of the cactus family, have the particularity of being able to store water in their young leaves, stems or roots. They must be able to absorb very large quantities of water in a short time, as rains are often of low intensity and do not last long, as soils dry quickly under the influence of intense sunlight. Almost all succulents have very long roots, developing horizontally on the surface to capture water resources most efficiently. Once this water has been absorbed and stored, it should not be lost, which is made possible by the reduction in size or even the absence of leaves. In addition, these leaves and stems are covered with a waxy cuticle that makes them practically impervious to the outside environment. At the physiological level, many succulent plants have a very efficient photosynthesis mode with respect to water called CAM for "*Crassulacean Acid Metabolism*" (see Focus [The House-leek](#)). CAM plants open their stomata at night to facilitate gas exchange, and thus store carbon dioxide which will be used by photosynthesis during the day while the stomata are closed, thus limiting water losses. Due to lower temperatures and higher humidity at night, CAM plants lose 10% less water per unit of carbohydrates, compared to plants whose gas exchanges occur with stomata that are open during the day (so-called C3 plants).

Drought tolerance is an ability of many plants in drylands. These plants are capable of undergoing desiccation (Action of drying out; drying out: drying out the soil, of a plant. Removal of water, natural or not, contained in a substance) without dying. Often, they lose their leaves during dry periods and enter a deep dormancy. The greatest water loss of a plant is through evapotranspiration through the surface of the leaves and stomata; therefore, the loss of leaves helps to preserve water in the stems. Some plants do not have this ability to lose their leaves, which are covered with resins that limit water evaporation. Unlike succulent plants that have a superficial root system, some desert trees and shrubs survive thanks to a highly developed root system, which can reach twice the surface of the canopy (Upper forest floor, directly influenced by solar radiation. Considered as a habitat or ecosystem as such, particularly in tropical forests where it is particularly rich in biodiversity and biological productivity.) and this to great depths. When heavy rains occur, the deep soil remains wet longer, allowing these plant species to grow in longer time steps. On the other hand, this type of plant can maintain photosynthetic activity even if there is very little or no water, which would be fatal to most plants in temperate zones.

A third type of plant found in deserts... simply does not exist most of the time because the conditions are too unfavourable. This

drought avoidance is possible in these annual plants, which use all their energy to produce seeds quickly, instead of maintaining their vegetative state for as long as possible. Fall conditions are often favourable in many deserts because of rainfall and falling temperatures. Non-dormant Property of an organism with a slower life phase where growth and development are temporarily stopped. seeds from annual plants can germinate quickly and massively and complete their entire life cycle in a few weeks. They then produce enough seeds to ensure the sustainability of the species before winter conditions set in.

These two examples of specialized flora adapted to survival in contrasting and hostile environments (taiga and deserts) clearly illustrate the role of **natural selection** in the **evolution of plant species best adapted to the particular, sometimes extreme, conditions of a given environment**. Over time, the **mutations** that have allowed the development most adapted to external conditions (e.g. leaf morphology, Figure 5) have been fixed in the species' **genomes** to ensure their sustainability in specific habitats.

3. The temporal adaptation of plants: storm warning!



Figure 6. Impact of a directional mechanical force (wind) on the development of a tree at the seaside [source: "Árvore da Preguiça-Jericoacoara" Photo credit: [homemadeluckyshots - part 2](#) via [Visual hunt \(CC BY-NC-SA 2.0\)](#)]

We have seen that plant species, through **evolutionary pressure**, have adapted to very diverse environments. Moreover, individuals of the same species show a very high degree of plasticity allowing them to adapt to the fluctuating conditions of the same habitat [9]. One of the most visible examples is trees found by the sea that are subjected to strong winds, often coming from the same direction, and creating severe mechanical stresses on their structure (Figure 6).

Extreme cases of drought adaptation are also remarkable, such as Jericho roses (*Selaginella lepidophylla*), more commonly referred to as resurrection plants that appear to be dead and "live" very quickly if they receive water (Figure 7).



Figure 7. The resurrection plant (Jericho rose, *Selaginella lepidophylla*) gives the appearance of being dry and dead in the absence of rainfall (A). As soon as rain falls, it regenerates very quickly and flowers to make seeds and reproduce (B); [source: © The Quantum biologist].

These two examples illustrate well the ability of plants to perceive the stressful external conditions of their environment, and to respond to them to adapt as well as possible. The perception of stress by plants and the biological responses that result from it have been the subject of intense research over the past twenty years. The development of molecular genetic Branch of biology and genetics, which consists of the analysis of gene function at the molecular level. {end-tooltip} and its coupling with analytical methods of biophysics, biochemistry and physiology have contributed to the development of an integrative plant biology. It has made it possible to understand the mechanisms of stress perception and transmission of this signal, which will lead to a re-programming of genetic expression and finally to the plant's phenotypic response to stress.

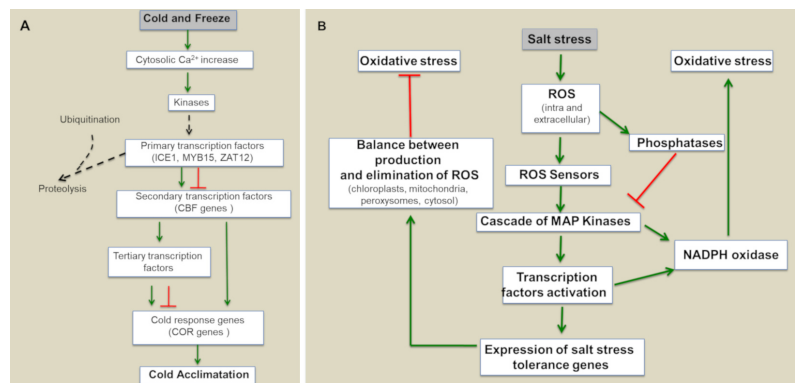


Figure 8. Diagrams illustrating the different stages of a plant's cellular and molecular responses to stress caused by cold (A) or excessive salt in the soil (B). A, Transcriptional cold response network. Cold induces the activation of primary transcription factors by modifying them post-transcriptionally by phosphorylation using kinases. Once activated, they then positively or negatively regulate the expression of secondary transcription factors, CBFs. These will activate the expression of tertiary transcription factors, and directly the expression of cold acclimatization genes (COR genes). Tertiary transcription factors also regulate the expression of COR genes, positively or negatively. When the cold stress is over, the return to equilibrium of the system is achieved through a post-transcriptional modification of the primary transcription factors, ubiquitination. This reaction leads the primary transcription factors to a proteolysis degradation pathway, thereby implying the repression of CBF gene expression. Red lines ending with a bar indicate negative regulation; green lines ending with an arrow indicate positive regulation. The dotted lines indicate post-transcriptional events. B, Network for regulating responses to saline stress. Red lines ending with a bar indicate negative regulation; green lines ending with an arrow indicate positive regulation. ROS = reactive oxygen species; MAP = Mitogen activated protein

Two examples of **signalling pathways** used by plants to adapt to particular stress conditions, cold or excess salt, are presented in Figure 8. When the cold occurs, a cascade of events occurs in the plant and will regulate the expression of cold response genes. First, the calcium concentration of their cytosol increases, which leads to the activation of a number of enzymes that modify transcription factors [10]. These factors then attach themselves to the DNA upstream of cold response genes, or their regulators, to activate or suppress their expression. When stress stops, the system returns to equilibrium through other post-transcriptional changes in certain transcription factors that cause them to be degraded by proteolysis (Figure 8A).

The response of plants to excess salt in their environment is determined by a balance between the production and elimination of activated forms of oxygen (ROS) such as hydrogen peroxide (H₂O₂), superoxide ion (O₂⁻) or the hydroxyl radical (-OH). The perception of these ROS by sensors activates kinases that will phosphorylate transcription factors, and thus activate them. The products of the response genes regulated by these transcription factors will lead to the elimination of ROS and therefore oxidative stress caused by excess salt. The balance is also determined by the fact that the activation of phosphatases will counterbalance the action of kinases, and that, conversely, the activation of oxidases will promote oxidative stress.

Many variations of the schemes presented in Figure 8 exist to reflect the specificity of a given stress, but the following **general principles** that are now widely accepted in the scientific community can be stated:

Stress will generate the production of **signals** by the plant.

These signals are often **small organic molecules** from metabolic activity, they can be:

- polysaccharides derived from the degradation of plant walls;
- lipid molecules resulting from the action of specific enzymes such as lipoxygenases, enzymes that catalyse the oxidation of fatty acids;
- small peptides capable of circulating in the sap developed to signal stress at long distances in the plant.

Some of these metabolites act as plant hormones, such as abscisic acid, which is considered a true stress hormone.

These signals are perceived by **receptors** that are often proteins located in the cell membrane; they have kinase or phosphatase activities, *i.e.* they remove or add phosphate groups.

In many cases, the **propagation** or **amplification of signals** requires the intervention of **secondary messengers**. Ca^{2+} ions and activated oxygen species (ROS) are the secondary messengers most regularly involved in plant responses to environmental variations.

These secondary messengers enable the **activation of cascades of** protein kinases and phosphatase proteins soluble in the cytoplasm and nucleus of cells.

in the end, the terminal targets of these reaction cascades are often **transcription factors**, capable of binding to DNA upstream of **stress response genes** whose expression they activate.

All the products of these genes (structural proteins, enzymes, etc.) allow the adaptive phenotypic response of plants to the stress they undergo.

In addition to this regulation of gene expression in response to environmental constraints, there is also **epigenetic regulation** [11],[12] (read [Epigenetics, the genome and its environment](#) & [Epigenetics: How the environment influences our genes](#)). As environmental variations often occur repeatedly, it is advantageous for plants to have a "memory" of these past events, and to use the storage of this information to adapt more effectively to new episodes. One of the best known examples concerns defence against herbivores, but these mechanisms also concern adaptation to abiotic stresses. Different means allow this memorization: accumulation of metabolic compounds, such as osmoprotectants to resist drought, phosphorylation / dephosphorylation of regulatory proteins as mentioned above. But much research has highlighted the importance of epigenetic regulation in adapting to different stresses, and in particular the role that small regulatory RNAs called miRNA and siRNA can play. Initially, epigenetic regulations allowing plants to adapt to environmental constraints were described in the case of adaptation to poor phosphorus and copper nutrition conditions. The role of these small RNAs has since been clarified for adaptation to drought or temperature increases. At a more integrated level, genes carried by DNA are packaged in the cell nucleus in a complex combining DNA and proteins called chromatin. The state of compaction of the chromatin determines the expression of genes. It is regulated by post-transcriptional modifications (methylation, acetylation, phosphorylation, etc.) of histones, proteins that structure DNA within chromatin (see [Epigenetics, the genome and its environment](#)). The stress conditions for the plants mentioned above are thus able to modify the structure of the chromatin in the vicinity of genes important for adaptation to these stresses. This process therefore contributes to the regulation of the expression of their stress genes and the adaptive response of plants [13].

4. The future of plant adaptation in the context of climate change

The **climate change** that our planet is currently experiencing is manifested by, among other things, temperature increases, a change in precipitation patterns and an increase in the concentration of CO_2 in the atmosphere. Drought and floods are known to influence plant biology. The adaptive phenomena of plants will therefore necessarily evolve in a multi-stress context with the increase in atmospheric CO_2 as a determining element [14].

Several studies have analysed the transcriptome (the mRNA repertoire, *i.e.* expressed genes), proteome (the protein repertoire) and metabolome (the metabolite repertoire) of different species exposed to high concentrations of CO_2 . Significant reprogramming at all these levels has been observed and mainly concerns photosynthesis and carbonaceous metabolism, as well as the biosynthesis of amino acids, starch and sugars. Another parameter that is being profoundly altered by climate change is plant nutrition. The increase in temperature and CO_2 concentration will affect the physiology of soil microorganisms and thus alter nutrient cycles and their availability for plant growth [15]. Experiments were thus carried out on plants grown at CO_2 concentrations equivalent to those expected in 2050. They showed that, under these conditions, the iron and zinc concentrations of C3 plant seeds are significantly reduced. The protein concentration of C3 plants is also decreasing due to the alteration of nitrogen nutrition at high CO_2 concentrations. However, plants with CAM metabolism are less constrained by these CO_2 increases.

This climatic evolution will therefore have the consequence of modifying the geographical distribution of certain species, and promoting the emergence of new adaptive processes, but also of influencing human activity by modifying the nutritional quality of plants [16]. This will have an impact on agricultural practices.

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L'Encyclopédie de l'environnement est publiée par l'Université Grenoble Alpes - www.univ-grenoble-alpes.fr

Pour citer cet article: **Auteur** : BRIAT Jean-François (2019), The fixed life of plants and its constraints, Encyclopédie de l'Environnement, [en ligne ISSN 2555-0950] url : <http://www.encyclopedie-environnement.org/?p=6942>

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