How do plants tolerate a salty diet?

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Soils can become naturally saline, for example due to sea spray. But they can also be saline due to human activities. The latter phenomenon is a problem affecting 20 to 30% of the 260 million hectares of irrigated land worldwide. A number of plants grow naturally in saline conditions, by the sea for example, despite the cellular toxicity of the sodium ion present in large quantities. However, the majority of plants - especially those used in agriculture, such as rice - are sensitive to excess salt in the soil. This is a food safety issue that is of concern to international research. Several decades of research have led to a good understanding of salinity toxicity and adaptive mechanisms in plants. This knowledge is now opportunely being put to good use to obtain new varieties of crops that are more tolerant to soil salinity; with, why not, cereal crops irrigated with salt water as a holy grail!

1. Plants and salt

1.1. Tolerant plants

Figure 1. Halophilic plants. A, Glasswort (Salicornia europaea); B, Sea spurge (Euphorbia paralias); C, Couch grass (Elymus farctus); D, Sea daffodil (Pancratium maritimum). [Source: A, Jürgen Howaldt / CC BY-SA 2.0 DE / B, Jean Tosti GNU license / C, Stephano / CC BY-NC-SA 2.0; D, Zeynel Cebeci / CC BY-SA 3.0]

Sea spray, made up of **seawater droplets** suspended in the **air**, **sprays** the vegetation on the seashore and salts the soil where it grows. This vegetation is called "**halophilic**" which means "salt-loving". [1] A "halophyte" is any plant that lives in contact with abnormally high concentrations of salt. Examples of halophytes are plants that grow in seashores, deserts, salt marshes, or salt lakes.

In the salt marshes you can find glasswort *(Salicornia sp.*), which includes about thirty edible species, and on the dunes the sea spurge (*Euphorbia paralias*), the sand Couch grass (*Elymus farctus*) or the magnificent sea daffodil *(Pancratium maritimum*).

Figure 2. Salt meadow sheep farm near Mont-Saint-Michel (Manche, France). [Source: Jean Paulo de Souza Henrique / CC BY-SA 4.0]

At other latitudes in humid tropical and equatorial climates, **mangrove** vegetation growing roots in brackish water illustrates the salinity tolerance capacities of halophilic grasses or shrubs.

Halophytes can tolerate salt concentrations in the range of 500 mM to 1 M, exacerbating the effectiveness of mechanisms for managing the toxicity of the sodium ion Na^+. [2] Some plants, such as glasswort, require this ion to grow, and these are known as strict halophytes.

These ungrateful ecosystems lend themselves to agriculture; for example, salt meadow pastoralism (Figure 2) provides an example of an agricultural practice with sheep raised and fed with halophilic flora adapted to soil salinity, flooding and drought, including Puccinellia *(Puccinellia maritima*, a grass), troscart (*Triglochin maritima*) or obione *(Halimione portulacoïdes*).

1.2. Sensitive plants

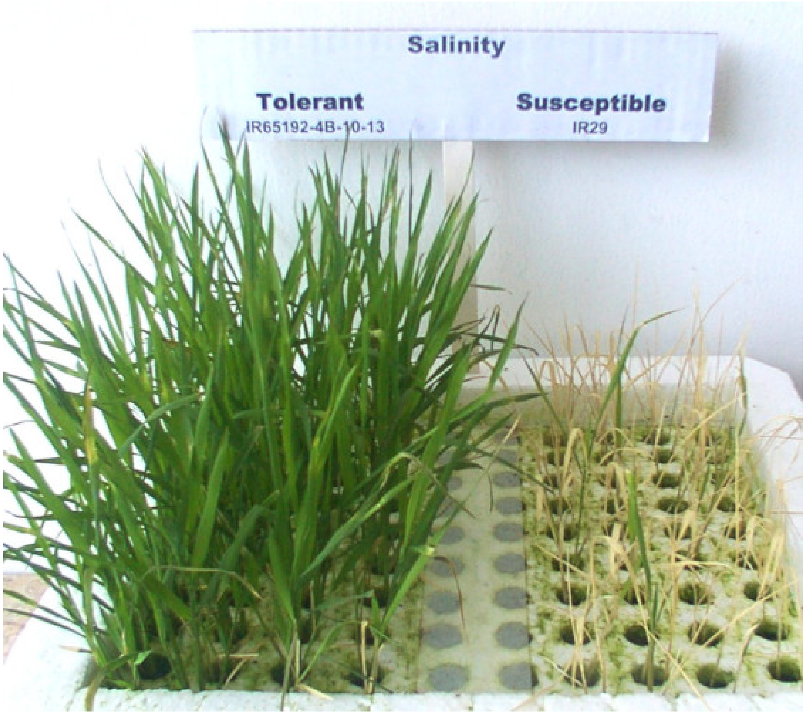

Figure 3. Leaf symptoms caused by Na^+ toxicity in rice plants. Salt-sensitive (right) and tolerant (left) cultivar are grown in hydroponic solution supplemented with NaCl. The sensitive cultivar shows significant growth retardation and burnt leaves. This variability in the level of salinity tolerance within the same species is used by research to identify genes and mechanisms that are responsible for tolerance. [Source: © International Rice Research Institute / CC BY-NC-SA 3.0]

While halophytes can grow on saline soils, other plants that are not adapted to these extreme conditions are unable to do so. These are **glycophilic** or "glycophytic" plants that grow in salt-free environments. Plant species have a wide range of **tolerance** to salt stress. For example, in the cereal group, rice *(Oryza sativa*) is the most sensitive (Figure 3), followed by durum wheat *(Triticum turgidum* ssp. *durum*), bread wheat (*Triticum aestivum*); barley *(Hordeum vulgare*) is the most tolerant [3].

The growth and development of glycophytes are affected in saline soils, due to the presence of excess soluble salts, mainly the sodium **cation** (Na^+). The visual symptoms of salt damage are **chlorosis** of the leaf tips, followed by leaf **scorch**, browning and leaf death. This results in **reduced** plant **growth**, stunted roots, **sterility** and reduced seed production.

The spread of soil salinization is a **major environmental problem**: every year, 10 million hectares of agricultural land are destroyed worldwide by soil salinization. Climate change, excessive use of groundwater, increasing use of poor quality irrigation water, massive irrigation in a semi-arid to arid climate zone and a lack of soil **leaching** can intensify this phenomenon of soil salinisation (See Focus on Soil Salinization). For several decades, research in plant biology has led to a much better understanding of the mechanisms of toxicity linked to salinity and those that enable plants to adapt to it (See Focus on Plant Biotechnology and Crop Salinity Tolerance).

2. Toxicity of Na^+ ion in plant cells

The Na^+ ion, in high concentration in the soil, leads to a series of deleterious processes for plant growth and development:

On the one hand, a high concentration of salt in the soil solution increases its **water potential** [4] ; this will disrupt plant water and nutrient **nutrition** via the roots.

On the other hand, the plant cannot prevent the long-term entry of Na^+ into its root cells and its translocation to the aerial part, causing **widespread cell intoxication**.

A two-phase model has been proposed to explain the deleterious mechanisms due to an excess of Na^+ ion:

early effects related to the increase in external **osmotic pressure**;

later effects related to the accumulation of **Na^+** in the cells.

2.1. Water, salt and water potential

The **presence of salt in the soil affects its water potential**. This potential is the energy that must be applied to the soil to release 1g of water. It is always negative, and the lower it is, the stronger the bond between water and soil is. [5] Pure water has a water potential of 0; but in soil, water is not pure and contains solutes, which are responsible for the decrease in water potential. It is therefore defined as follows:

by its **water content**. Thus a well hydrated soil will have a water potential with values of about -0.1 MPa, while a dry soil will have values of about -1 MPa.

by the **solute concentration** of the soil. Thus, this value can reach about -0.4 MPa in a soil contaminated with a 150 mM NaCl salt solution.

To understand the importance of these physico-chemical parameters in salinity problems, the water potential of the root cells must be taken into account. Under normal conditions, root cells have a water potential value of about -0.5 MPa.

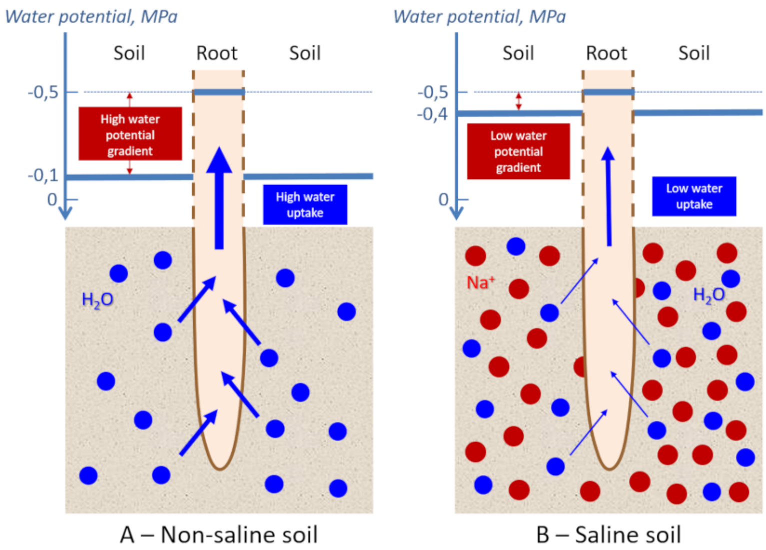

Figure 4. In saline soil, the osmotic pressure associated with salt reduces the difference in water potential between the soil and the root. As a consequence, the flow of water into the root is decreased. This reduces the water available to the plant for growth and yield. [Source: EEnv scheme adapted from Rengasamy et al., ref. 7]

The movement of water goes from the **highest** potential **to** the **lowest** potential (in other words from the least negative to the most negative). The difference in water potential between soil and plant cells (0.4 MPa) will allow water to move from the soil (-0.1 MPa) to the root cells (-0.5 MPa) (Figure 4A). [6]

When soil is contaminated with a 150 mM NaCl salt solution, this difference in water potential is reduced to 0.1 MPa (Figure 4B). This difference in water potential is one of the driving forces behind the flow of water through the cell membrane. It can be estimated that, apart from any adaptive cellular response to salinity, this driving force is 4 times less efficient in transferring water from the soil to the root interior under salinity conditions than under normal conditions!

In an extreme situation where the soil salinity would be higher, one could theoretically witness the exit of water from the root cells into the saline soil, and dehydration of the plant by its roots! This phenomenon is reminiscent of **hydric stress** which can have several causes (drought, frost, ...) and occurs when the soil is not able to supply enough liquid water to the roots to ensure tissue hydration and evaporation by the leaves (See The fixed life of plants and its constraints).

Damage due to the osmotic effect of salinity not only impacts the turgidity of the cells, but induces **metabolic changes** similar to those caused by water stress. For example, osmotic stress has an immediate effect on the **growth** rate of **plants**.

2.2. Salinity, photosynthesis and oxidative stress

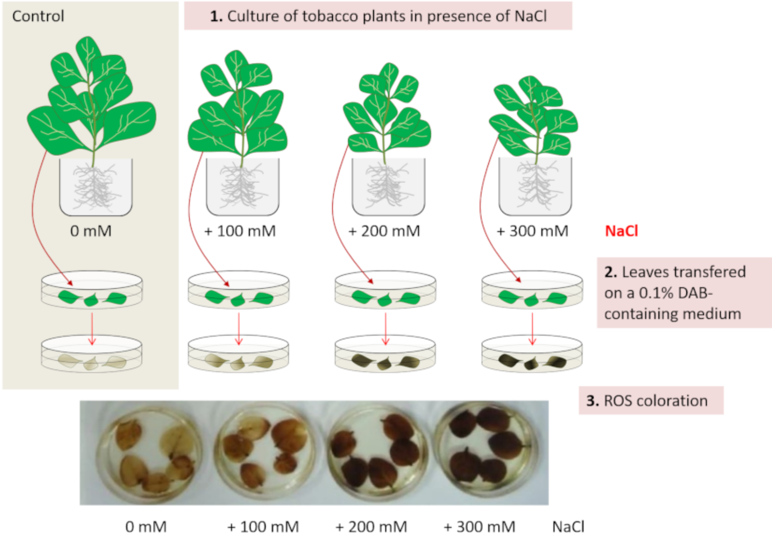

Figure 5. Staining of tobacco leaves revealing the accumulation of Reactive Oxygen Species or ROS (H_2O_2). Tobacco plants were grown for 60 days in a medium with or without NaCl (top diagram). The leaves were then transferred to Petri dishes containing 3,3′-diaminobenzidine (DAB). DAB allows visualization of H_2O_2 accumulation in tissues grown in the presence of NaCl.

In addition to suffering osmotic stress that prevents normal water absorption at the root cell level, the plant must also deal with disorders in its **leaf parts**:

Photosynthesis is altered, due to the **stomata** closure, a phenomenon controlled by the hormone abscisic acid, and the inhibition of CO_2 fixation;

The linear transfer of electrons through photosystem II is inhibited, the cyclic transfer of electrons within photosystem I is activated;

The non-photochemical quenching **protection** mechanism set up to evacuate excess light energy in the form of fluorescence is exacerbated [7] (See Focus Z as photosynthesis).

The immediate consequence of these disorders in photosynthesis is the production of **Reactive Oxygen Species** (**ROS**, for Reactive Oxygen Species) and the expression of enzymes involved in the management of **oxidative stress** to prevent damage to photosystems, lipids, proteins and nucleic acids. However, one of the ROS, **hydrogen peroxide** (H_2O_2), also has a cell signalling role in salt tolerance. Thus, there is a **coordination** mechanism between the ROS production, their elimination by enzymes and a sufficient amount required for cell signalling (Figure 5). [8]

2.3. Why is Na^+ toxic?

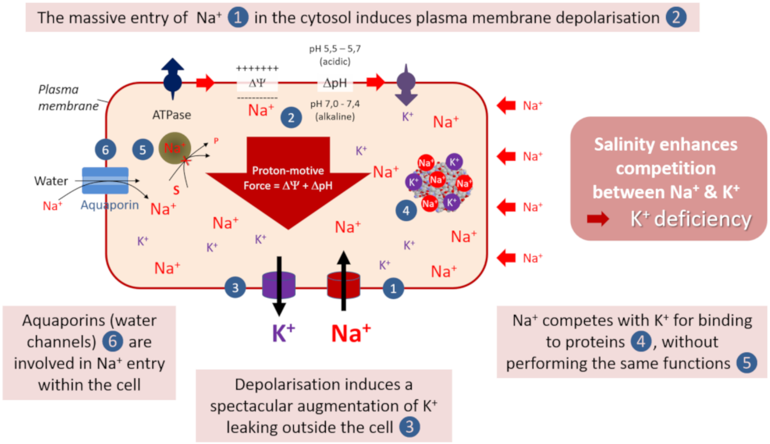

Figure 6. Impact of Na+ on plant cell function under conditions of salt stress. [Source: © EEnv diagram]

The specific toxicity of the Na^+ ion could be due to its physicochemical properties that are close to those of K^+ (**Potassium**). In all living organisms, K^+ is the main inorganic cation in the **cytosol**, where its concentration (about 0.1 M) is generally several times higher than that of Na^+. It plays an essential role in plant physiology. Due to its intracellular abundance, it is the major inorganic counter-ion to the negative charges of proteins and nucleic acids, with in particular functions to activate more than **fifty enzymatic reactions** [9] (See Focus Potassium and Sodium: fraternal twins!).

The massive entry of Na^+ into the cytosol of plants in a saline environment leads to a series of reactions (Figure 6). [10]

Na^+ competes with K^+ for the absorption of the latter in the root cell, as both ions are transported across the plasma membrane by several identical transport systems (NSCC-type non-selective cation channels and HKT high-affinity transporters). This phenomenon is **exacerbated in a saline stress situation**.

Na^+ has deleterious effects on the cell surface as it **severely disrupts the electrical polarization** of the plasma membrane. This depolarization leads to a dramatic increase in **K^+ leakage** outside the cell, through the K^+ channels activated by depolarization (channels called KOR).

Na^+ would compete with K^+ in **binding to important proteins**, without performing the same functions as the latter. An excess of Na^+ in the cytosol would thus **inhibit** the **activity** of numerous **enzymatic reactions** leading to cellular dysfunction, for example on the photosynthetic activity of plants.

Recent data indicate that the **aquaporins** (water channels) of the plasma membrane, known mainly for their activity in transporting water and neutral solutes, also participate in the **entry of Na^+** into the cell!

Thus, **despite the presence of K^+ in the soil**, one can say that salinity causes a **deficiency of this nutrient** in the plant!

3. Salinity tolerance mechanisms in plants

3.1. What is salinity stress?

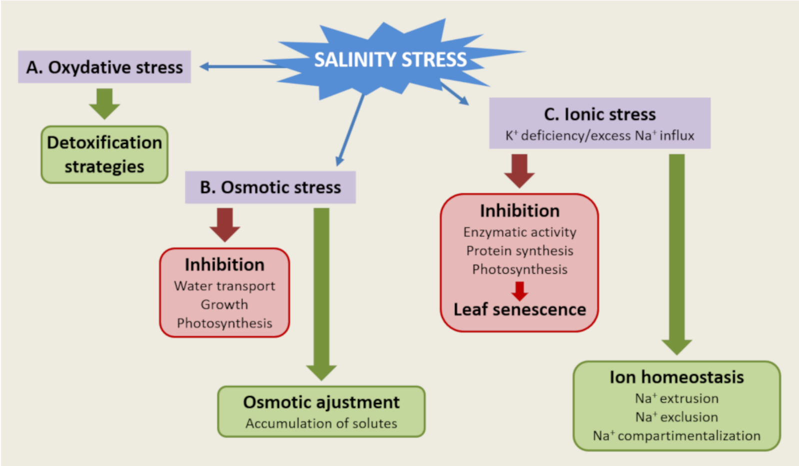

Figure 7. Deleterious effects related to salinity stress toxicity and the cellular response set up to ensure tolerance. In halophilic plants, excess salt in the soil causes ionic, oxidative and osmotic stress, which they must manage by implementing strategies to maintain (A) oxidative stress molecules at an acceptable level, (B) osmotic balance, and (C) ionic homeostasis. [Source: © EEnv diagram]

Plants have developed several biochemical and molecular mechanisms to resist the adverse effects of soil salinity. The components of a saline stress can be grouped into three categories [11]:

The **oxidative stress** encountered during salinity stress must be managed at the cellular level by protective and damage repair mechanisms.

The response to **osmotic stress** makes it possible to maintain water homeostasis through biosynthesis of **compatible solutes** and the involvement of aquaporins (water channels).

These mechanisms involve the function and regulation of Na^+ and/or K^+ transport systems involved in the response to **ionic stress** (Figure 7). [12]

3.2. Detoxification strategies against oxidative stress

Oxidative stress, caused by salt stress, in corn seedlings was observed mainly in the mature roots and leaves, and to a lesser extent in the young leaves (Figure 7A). Various **detoxification strategies** are then put in place :

Increase in H_2O_2 content and markers of **oxidative damage to** cell membranes (electrolyte leakage and lipid peroxidation).

Accumulation in cells of **antioxidant molecules** (polyphenols, flavonoids, ascorbate, ...) and antioxidant enzymatic activities (catalase, superoxide dismutase, peroxidase).

In this way, ROS protection mechanisms can be activated throughout the plant, as is the case in many other stress situations (See How do plants cope with alpine stresses?).

3.3. How can water homeostasis be maintained?

Maintaining water balance in the plant tissues (also called water homeostasis) is crucial for plant growth and development. Water is lost through **transpiration** through the stomata and acquired through **root absorption**. Water homeostasis is therefore ensured by the supply of water, but also by the capacity of plant cells to **retain water**.

Under conditions of osmotic stress, water homeostasis is disturbed (see Figure 4), the plant cell accumulates compatible solutes in the cytosol to **balance the osmotic pressure** (Figure 7). These are sucrose, proline and glycine betaine. For example, the accumulation of proline has been described as a **non-toxic and protective osmolyte** in a large number of plants under salt stress.

3.4. Maintaining ionic balance?

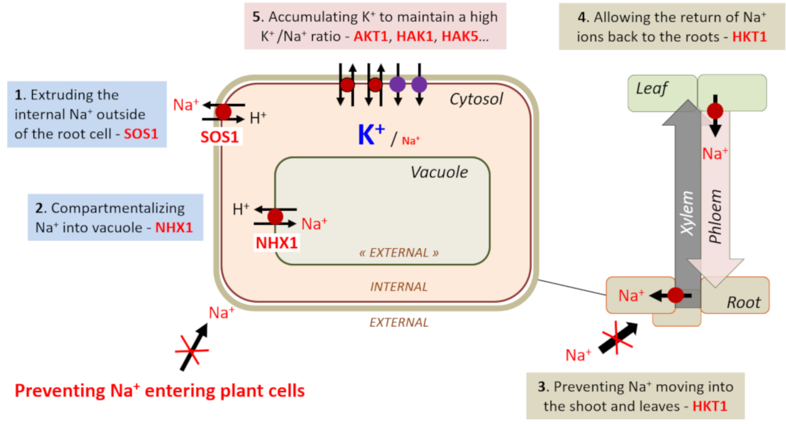

Figure 8. Strategies involved in ionic homeostasis implemented in root cells by plants to enable them to tolerate saline stress. [Source: © EEnv diagram]

Analysis of the rice genome has identified genes responsible for **salt tolerance** in rice [13]. One of them encodes an Na^+ transporter involved in homeostasis between K^+, an essential element, and Na^+, a toxic element. This major discovery highlights the importance of the **transport systems** of these two ions in the phenomenon of salt tolerance.

For a plant to be able to tolerate salt stress, it is important that the **K^+/Na^+ ratio** in root cells cytosol is **high** and therefore that these cells contain little Na^+ (Figure 7C). Different strategies enable plants to achieve this; they involve transport systems that contribute to Na^+ and K^+ homeostasis (Figure 8).

Extruding excess Na^+ ions from the root epidermal cells to the **outside**. The protein called SOS1 [14] plays a role in this process, it is the only system of localized Na^+ efflux at the plasma membrane characterized so far in plants.

Compartmentalizing of Na^+ ions into the vacuole, once they are in the cytosol, by the activity of the NHX1 protein [15].

Preventing translocation of Na^+ ions to aerial parts. This role is performed by a selective Na+ influx transporter of the HKT1 family. Located in the root **xylem** parenchyma, it allows the discharge of Na^+ from the xylem sap, by retaining this ion in the cells of the xylem parenchyma. The *Saltol* locus carries the gene encoding this transport system.

Allowing the return of Na^+ ions back to the roots. HKT1 is also expressed in cells adjacent to the phloem vessels in leaves; this would allow recirculation of Na+ from the aerial parts, loading the Na+ into the phloem to allow return.

Counteracting the toxic effects of Na^+ through the involvement of K^+ transport systems. These systems help to maintain a high cytosolic K^+/Na^+ ratio. For example, in rice, individual mutations in the *AKT1*, *HAK1* and *HAK5* genes, encoding, respectively, one and two K^+ transporters, cause a higher sensitivity to saline stress in mutated plants. This demonstrates that K^+ nutrition plays a major role in soil salinity tolerance (Figure 8).

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4. Sodium can be useful to plants!

Figure 9. Atriplex vesicaria, a shrub from the arid and saline soils of Australia, needs salt for its growth. [Source: Mark Marathon / CC BY-SA 4.0]

Despite its toxicity in plants, the sodium ion (Na^+) is also a nutrient, especially when the potassium ion (K^+) is in low concentration in the soil.

K^+ concentration in the soil in the **millimolar** range allows **optimal** plant **growth**. The availability of K^+ ions in the soil solution, slowly released by soil particles and clays, is often limiting for optimal growth in most natural ecosystems. When the K^+ concentration in the soil is very low, of the order of the **micromolar**, **Na^+ can substitute it** in certain vital functions, such as its role as a solute to maintain osmolarity in the cell (See Focus Potassium and Sodium: fraternal twins!).

About 90% of the K^+ is stored in the **vacuole** where it plays an osmotic role. Confined in the vacuole, Na^+ can play the same role; the cell then mobilizes K^+ in the cytosol where it performs its metabolic role. A Na^+ transport system specifically expressed when the K^+ concentration in the soil is low would allow Na^+ to be absorbed into the plant for this beneficial use [16]. Na^+ can thus stimulate plant growth at **low concentrations**.

Halophilic plants may need certain concentrations of NaCl to grow properly, as in *Atriplex vesicaria* (an Australian shrub closely related to the obione *Halimione portulacoïdes* found in salt meadows in France, Figure 9), *Echinochloa utilis* (Japanese millet) or *Portulaca grandiflora* (a purslane).

5. Messages to remember

Worldwide, **20% of irrigated land** is threatened by progressive soil **salinization**:
- plants of agronomic interest have little or no tolerance to soil salinity ;
- only halophilic vegetation is adapted to grow in saline conditions.

The **sodium ion (Na^+)** is the main cause of **toxicity** due to salt disturbance :
- water and nutrient uptake by the roots;
- photosynthesis in the leaves;
- but also by accumulating activated forms of oxygen leading to oxidative stress.

Due to their similar physico-chemical properties, Na^+ **competes with the potassium (K^+) ion**, a major nutrient in plants.

Plants react to the presence of Na^+ in several steps:
- By **protecting** themselves against oxidative stress;
- By accumulating solutes to **counteract the osmotic effect of** too much Na+ in the soil;
- By **limiting the absorption of Na^+** in the root, increasing its **expulsion** outside the root cells, **confining it to** the vacuole, and managing its **transport** and exclusion from the leaves. The plant also improves its K^+ nutrition.

Notes and References

Cover image. Rice field in Cat Bà (Vietnam). [Source: © Doan Trung Luu]

[1] Halophilic plants are also referred to as halophilic plants, as opposed to glycophilic or "glycophytic" plants that grow in salt-free environments.

[2] Flowers T.J., Galal H.K., & Bromham L. (2010). Evolution of halophytes: multiple origins of salt tolerance in land plants. *Funct. Plant Biol.* 37, 604-612. doi: 10.1071/FP09269

[3] Munns R. & Tester M. (2008) Mechanisms of Salinity Tolerance. *Ann. Review Plant Biol.* 59: 651-681

[4] L'eau, de l'absorption à la transpiration (in French)

[5] It is expressed in pressure units such as Pascal (Pa)

[6] Rengasamy P., North S. & Smith A. (2010) Diagnosis and management of sodicity and salinity in soil and water in the Murray Irrigation region. The University of Adelaide, SA.

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[9] Bhandal I.S. & Malik C.P. (1988) Potassium estimation, uptake, and its role in the physiology and metabolism of flowering

plants. *Int. Rev. Cytol.* 110: 205-254

[10] The general outlines of this article are original, but inspired by many pedagogical schemes. The most emblematic of them is "*Teaching tools in Plant Biology* (2014) Plant Nutrition 1: Membrane transport and Energetics, Potassium nutrition, and Sodium toxicity. DOI: https://doi.org/10.1105/tpc.114.tt0914."

[11] Munns R. & Tester M. (2008) Mechanisms of Salinity Tolerance. *Annu. Rev. Plant Biol.* 59, 651-681.

[12] Plant Nutrition 1: Membrane Transport and Energetics, Potassium Nutrition, and Sodium Toxicity

[13] This gene is called *Saltol* (for *Salt Tolerance*). It encodes a selective Na^+ influx transporter of the HKT1 family. The rice genome was fully sequenced in 2005. Its repertoire of some 37,500 genes is now available. Any visible and measurable agronomic trait (the phenotype), such as tolerance to drought, salinity or plant height, can be associated with a set of genes (the genotype).

[14] SOS1 for *Salt Overly Sensitive* ; this is a Na^+/H^+ antiport. An antiport is a membrane protein involved in the active transport of different ions across a membrane, such as the plasma membrane, in opposite directions Na^+ in one direction and H^+ in the other.

[15] This is a Na^+/H^+ antiport of the NHX1 type.

[16] Horie T., Costa A., Kim T. H., Han M.J., Horie R., Leung H.-Y., Miyao A., Hirochika H., An G. & Schroeder J.I., (2007) Rice OsHKT2;1 transport mediates large Na^+ influx component into K^+-starved roots for growth. *EMBO J.* 26, 3003-3014.

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