ELUCIDATING THE ROLE OF SODIUM IN SOILS AND PLANTS: A BOON OR A BANE?

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Sodium (Na), which is an integral constituent of Earth's crust, is one of the beneficial elements in soil. It is the sixth most abundant element and constitutes around 3% of Earth's crust. However, Na content seldom exceeds 1% in soils. It is an abundant solute in ocean water after chloride. In oceans, the Na concentration is near 470 mM which can be still higher depending on the rate of rainfall and evaporation. Na bearing minerals include plagioclase feldspars ($NaAlSi_3O_8$), micas, pyroxenes, and amphiboles. Na reaches soil by through the weathering process of these minerals, and occurs as NaCl, Na_2SO_4, $NaHCO_3$ and Na_2CO_3 in saline and saline alkali soils.

The role of Na in plant nutrition is still unexplained and ambiguous. According to Arnon's criteria of essentiality, Na is not considered as an essential element for plant nutrition but in several occasions its presence proved advantageous over some other essential elements at a short period of time for the growth of plants. This shows that there will be a threshold limit in all plants to take up Na and use it for the survival and growth of plants. This threshold limit may vary between plants depending on its internal make up. This article deals with roles of Na in plant growth, its concentration in soil, toxicity, uptake and physiological mechanisms involved in Na accumulation as well as efflux.

FUNCTIONS OF SODIUM IN PLANTS

Though Na is not considered as an essential element for most of the plants, at lower concentrations it favours growth and development of some plants. For example, subgroup of C_4 plants like Atriplex *spp*, *Kochia childsii*, millet, and a number of other C_4 grasses require Na for a physiological process, thus, giving Na an "essential element" status. However, Na can never be considered "nutritious" for most of the other plant species. Another group of plants that can tolerate salinity is halophytes. Higher Na^+ concentration promote growth of these plants (eg. *Suaeda maritima* and *Salicornia spp.*). Na can be an essential element to plants under certain conditions such as that of potassium (K) deficiency. Na and K have similarities in chemical, structural and ionic properties. During K^+ deficiency, many (glycophytic) plants respond positively to Na^+ fertilization. Na gets accumulated mainly in the cell vacuoles. Major roles of Na in plant nutrition are listed here.

1. Na maintains the solute potential of the cell
2. In case of K deficiency, Na can replace its functions in certain plants like sugar beet, table beet, turnip *etc*.
3. Na improves the water balance of plants under limited water supply or under arid climatic conditions

In case of salinity conditions, plants develop salt stress under prolonged exposure. The plants often express symptoms of K deficiency too.

SODIUM IN SOILS

Na saturation in soils is expressed as Exchangeable Sodium Percentage (ESP) and Sodium Adsorption Ratio (SAR) in soil solution. SAR is the relative proportion of Na^+ ions with respect to Ca^{2+} + Mg^{2+} ions in the soil solution. The formulae of ESP and SAR are as given here.

ESP = 100 (Exchangeable Na^+ ions/CEC); where all cations and CEC in mmol (+) kg^{-1} of soil]

SAR = $[Na^+]/\sqrt{(Ca^{2+} + Mg^{2+})/2}$; where all concentrations are in mmol (+) /L.

Another term is ESR, which indicate the exchangeable sodium ratio and it is related to ESP as given by

ESP = 100 (ESR)/(1+ESR) assuming CEC~$X_{Na^+} + X_{Ca^{2+}} + X_{Mg^{2+}}$.

Sodic soils are characterized by higher concentration of sodium ions on the exchangeable complex and in the soil solution. Soils with pH >8.5, ESP >15 and ECe <4 dS m^{-1} are categorized as alkali soils or sodic soils. Development of these soils will be under arid, semi-arid climatic conditions with excess evapotranspiration than rainfall (Oliviera et al., 2009).

EXCESS SODIUM IN SOILS AND PLANTS

Higher concentrations of Na, either in soil or in any growing medium are toxic. Excess content of Na in soil affects physical and chemical properties of the soil. Higher Na^+ content in soil crfeate following problems

1. Na, a dispersing agent causes dispersion of clay particles, resulting in poor soil structure, thus hinders penetration of roots, decreases seedling establishment and restricts movement of water.
2. Dispersed clay particles form a dense or compact layer and that decreases the permeability of soils.
3. Increased ESP decreases hydraulic conductivity
4. Surface crusting results clogging of soil pores
5. These soils remain very hard when dry and sticky when wet

Though glycophytes (sodium sensitive crops) respond to Na fertilization and are found to be benefitted from low levels of Na concentrations, excess sodium is toxic to most of these plants too. However, halophytes grow well with high concentration of Na^+.

Higher Na^+ in plants

1. Lowers water potential and create osmotic stress
2. Increased uptake of Na^+ negatively affects cellular biochemistry
3. Translocates excess Na^+ into shoot tissues eventually leading to plant death
4. Disturbs acquisition and distribution of essential nutrients such as K^+, $Ca^{2+}$and NO_3^-;
5. Disrupts both cellular and whole-plant potassium homeostasis.

UPTAKE OF SODIUM IN PLANTS

Based on the salt sensitivity, plants are broadly classified into glycophytes (sensitive to salt) and halophytes (salt tolerant). In general Na uptake is desirable up to some limit as it is a viable way to develop osmotic potential, sustain turgor pressure and also for the absorption of water. The chemical and electrical driving forces generated by the differences of activity and charge across the membrane help an ion to move across a membrane. The chemical driving force of Na in the plasma membrane may vary with the salinity. This chemical driving force will be larger when there is a high salinity and to withstand salinity the ratio of Na concentration across the plasma lemma might increase many fold (Blumwald et al., 2000). There are unrelenting dissimilarities between the Na^+ transport mechanisms of sensitive glycophytes and halophytes.

The entry of Na from a saline environment to plant cells is a passive process and its transport across the plasma membrane must be keyed up by the P type ATPases and supposed to be assisted by the plasma membrane Na^+/H^+ antiporter (SOS1).

The initial entry of Na ions from the soil solution to the plant system is through the cells of root epidermis and cortex. This unidirectional movement of Na ions from the soil to the plant is termed as the Na^+ influx and this movement is entirely different from the net Na accumulation or net Na^+ influx. This initial influx is the determining factor of the net Na accumulation in the upper parts of the plants. This Na influx is explained based on three pathways as proposed by Tester and Davenport (2003). Among that, two are the non-selective cation channel pathways mediated by two proteins and the third pathway emerges due to the 'leakage' through the apoplast into the roots. The non-selective channels include the cyclic nucleotide-gated channels (CNGCs) and glutamate receptors (GLRs). Aquaporins (AQP), the channels for the transport of water, also reported to involve in the Na^+ uptake in plants. Among the non-selective cation channels, the voltage insensitive non-selective channels are responsible to the influx of Na ions into the roots. But the presence of Ca^{2+} found to inhibit partially the Na^+ influx into the root tissues. The long distance transport of the Na inside the plant system is facilitated by the apoplastic or the symplastic pathways. The movement of Na partially through the root apoplast, and wherever the movement across the endodermis and exodermis needed the Na might cross these membranes via the bypass flow through the symplast. The application of silicon can reduce this apoplastic bypass flow of Na ions (Shi et al., 2013).

Analogous to Na in animals, the preferred cation for maintaining the cell potential in plants is K. The major K transporter proteins in plants are highly selective for K, but it can also transport Na with a low affinity. Since the ionic radii of Na and K are similar, the K transporters in plant system do not discriminate between these two cations. The main K transporters in plants are the high affinity K^+ uptake transporter (HAK), K^+ transporter (KT), the K^+ uptake transporter, the high affinity K transporter (HKT) and its homologs (Maser et al., 2002) and the non-selective cation channels (NSCCs). As a result of the non-selective mechanisms of the transporter proteins and channels Na^+ ions compete with K^+ ions under high salinity environments and enter into the plant system. These transporter genes are up or down regulated depending on the response to salt stress at transcriptional level.

SALINITY STRESS & K^+/Na^+ HOMEOSTASIS

Due to the ionic similarity, Na ions compete with K ions for entering into plant system. Under saline growth conditions this will results in dual injury *i.e.*, K deficiency and Na toxicity (Elumalai et al., 2002). Hence, under such Na stress situations, in order to maintain sufficient K nutrition plants have to activate a highly sensitive K uptake mechanism. It is a very common fact that when exposed to salty environment plants take more Na than K. But to alleviate the toxic effect of Na accumulation in the cytosol it is necessary to maintain a high K^+/Na^+ ratio in cytosol. The most important ways to reduce the Na toxicity is the compartmentalization of Na ion in the vacuole and starting the extrusion of Na at the root -soil interfaces. To facilitate this, the Na^+/H^+ antiporters present in the plasma membrane and vacuolar membrane and high H^+ gradients created by active H^+-pumps are very important. The mutual beneficial effects of NHX1, SOS1 and HKT1;5 have been anticipated to control the Na^+ homeostasis in the halophytes.

SODIUM ACCUMULATION AND SODIUM EFFLUX

Na efflux is the major mechanism through which plants control the rise in Na concentration in the cytosols of the root cells. Na efflux is an energy driven (active) pumping process by Na^+/H^+ transporter and H^+ - ATPases present in the plasma membrane (Zhu et al., 2009).The electrochemical proton gradient generated by the exclusion of H^+ by the H^+ - ATPases using the energy (ATP). This electrochemical proton gradient is used by the Na^+/H^+ transporter to exclude the Na^+ from the plant cells. This exclusion mechanism was reported in many plants (Blumwald et al., 2000).

The most important mechanisms responsible for the tolerance of excess Na in plants are the Na^+ efflux transporters and the Na^+ transporters that arbitrate Na^+ compartmentalization into vacuoles (Blumwald and Poole, 1987). Compartmentalization of Na ions especially in the vacuole of the plant tissues helps to reduce the toxic effects of high concentration of Na in the cytosol. This process is regulated by the vacuolar Na^+/H^+ exchangers (NHXs). This excess Na^+ accumulated in the vacuole guards the vital enzymatic reactions taking place in the cytoplasm, by maintaining turgor using the excess Na^+ available in the vacuole (Glenn et al., 1999).

CONCLUSION

Sodium in plants have a beneficial role when its concentration is comparatively low and studies revealed that the substitution of K with Na is possible even up to the 50% of the requirement from the external sources in some of the glycophytic plants (Neenu et al., 2012). Under saline environment to exclude the excess Na and maintaining a healthy K^+/Na^+ ratio both halophytes and the glycophytes follow desired pathways to protect the plant cells from the Na toxicity. A collaborative study between physiological, biochemical, genomic, genetic, and molecular biological disciplines helped to identify and characterize of important Na^+ transporter genes and proteins and the possible mechanisms of Na transport in the system. Further researches may lead to the development of transgenic plants which can survive under saline environments and will provide a clear picture about the role of Na in plants.

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