

Mechanism underlying the uptake of Na⁺, K⁺ and Cl⁻ under salinity stress- A review

Bulbul Ahmed^{1*}, Akbar Hossain², Tanushree Halder³, Mousumi Sultana⁴, Deepen Tamang⁵, Sushil Kumar⁵, Apurba Pal⁵, Jahnavi Sen⁵, Sabrina Shabnam⁶ and Debjani Dutta⁶

¹Plant Physiology Division, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur-1701, Bangladesh

²Agronomy Division, Wheat Research Centre, Dinajpur-5200, Bangladesh

³Department of Genetics and Plant Breeding, Sher-e-Bangla Agricultural University, Dhaka-1207, Bangladesh

⁴Tuber Research Sub Centre, Bangladesh Agricultural Research Institute, Bogra-5800, Bangladesh

⁵Department of Plant Physiology, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, Nadia, West Bengal, India

⁶Department of Agricultural Chemistry, Hajee Mohammad Danesh Science and Technology University, Dinajpur-5200, Bangladesh

ARTICLE INFO

ABSTRACT

Article history

Accepted 21 November 2016

Online release 30 April 2017

Keyword

Ion
Homostasis
Sodium
Potassium
Chlorine

*Corresponding Author

Name: Bulbul Ahmed

E-mail: kbdahmed@gmail.com

Na⁺ concentrations in the cytoplasm can lead to enzyme inhibition, which in turn causes necrosis and chlorosis while low extracellular Na⁺ concentrations will establish a large Na⁺ electrochemical potential gradient. Excess sodium in the soil limits the uptake of water due to decreased water potential, which may result in wilting. The contribution of Na⁺ to the leaf osmotic potential (9s) was sharply enhanced from 2% in control plants to 49% in plants subjected to 400 mM NaCl. *Atriplex canescens* is able to enhance photosynthetic capacity, increase Na⁺ accumulation in tissues and salt bladders, maintain relative K⁺ homeostasis in leaves, and use inorganic ions and compatible solutes for osmotic adjustment which may contribute to the improvement of water status in plant. The strategies for maintaining a high K⁺/Na⁺ ratio in the cytosol include sodium extrusion and/or sodium compartmentation. Xylem Na⁺ loading, and better K⁺ retention, is an efficient control over stomatal development and aperture. K⁺ involves in the process include the formation of carbohydrates and proteins, the regulation of internal plant moisture, as a catalyst and condensing agent of complex substances, as an accelerator of enzyme action, and as contributor to photosynthesis, especially under low light intensity where deficiency may result in higher risk of pathogens, wilting, chlorosis, brown spotting, and higher chances of damage from frost and heat. The compartmentation of Na⁺ and Cl⁻ into the vacuole allows plants to use NaCl as an osmoticum to maintain an osmotic potential that drives water into the cells.

Introduction

Sodium and chloride are typically viewed as waste ions that plants do not need. This can be true if their levels are high in a water source; however, research has shown that plants do use these elements in small quantities. Now before anyone raids the spice rack for the table salt and add it to your fertilizer stock tank, most water sources contain sufficient levels of both elements so their deficiencies are rare. Sodium is not an essential element for plants but can be used in small quantities, similar to micronutrients, to aid in metabolism and synthesis of chlorophyll. In some plants, it can be used as a partial replacement for potassium and aids in the opening and closing of stomata, which helps regulate internal water balance. Chloride is needed in small quantities and aids in plant metabolism, photosynthesis, osmosis (movement of water in and out of plant cells) and ionic balance within the cell. Sodium deficiency does not appear to exhibit any symptoms since it is not an essential element. Chloride deficiency can occur if there is consistently less than 2 ppm chloride in the growing medium and the symptoms appear as chlorotic blotches with necrotic spots located between the veins or on the margins of the younger leaves.

In advanced cases, chloride deficiency could cause plant wilting. Both deficiencies rarely occur since most water sources provide them and fertilizers often have them as impurities. Sodium toxicity appears as necrosis or scorching of the leaf tips and margins, similar to micronutrient toxicities. Chloride toxicity starts as premature yellowing of leaves then it leads to marginal or tip necrosis of older leaves and also bronzing. Geraniums, lettuce and poinsettias are sensitive to chloride toxicity while carnation, penstemon, tomato and verbena are less sensitive. Since both elements can be present in high, but not toxic levels in the growing medium, they can compete with beneficial fertilizer elements for uptake by plant roots. Sodium competes with potassium, calcium, magnesium and ammonium for uptake by the plant. Chloride can compete with nitrate, phosphate and sulfate uptake. Therefore, if sodium or chloride is high in the growing medium, while other beneficial elements are at low or normal levels, the plant, which cannot tell them apart, will take up what is in the growing medium. Therefore the plant may not acquire sufficient levels of a required beneficial element and can lead to its deficiency in the tissue. If sodium or chloride levels are high to excessive in the growing medium, it is most likely coming from the water.

Problems can occur if sodium and chloride levels in water exceed 50 and 70 ppm, respectively. If so, it is important to allow water to run out the bottom of each container at every watering to minimize build up of these elements. Also fertility levels cannot drop below normal levels as these waste ions will be absorbed in higher ratios vs. desired fertilizer elements. Monitor the salt levels in the growing medium at least every one to two weeks as they can quickly build up. If sodium or chloride levels in the water exceed 150 or 200 ppm, respectively, then reverse osmosis is the best option. Where to Find Sodium and Chloride: Both are normally found in sufficient levels in most water sources. If not, then sodium can be found in trace levels in fertilizers and certain pesticides. Chloride can be provided by fertilizer in the forms of calcium chloride, potassium chloride, ammonium chloride or magnesium chloride. This review the available research on the mechanism underlying the uptake of Na^+ , K^+ and Cl^- by plant parts under salinity stress condition.

Na^+ in plant shoot, leaf and root

At the plasma membrane, the chemical driving force for Na^+ will vary depending on the salinity. Given the negative electrical membrane potential difference across the plasma membrane (-140 mV), even low extracellular Na^+ concentrations will establish a large Na^+ electrochemical potential gradient that will favor the passive transport of sodium from the environment into the cytosol (Blumwald et al., 2000). Kering (2008) illustrated that in C4 plants, sodium is a micronutrient that aids in metabolism, specifically in regeneration of phosphoenol pyruvate (involved in the biosynthesis of various aromatic compounds, and in carbon fixation) and synthesis of chlorophyll). In others, it substitutes for potassium in several roles, such as maintaining turgor pressure and aiding in the opening and closing of stomata (Subbarao et al., 2003). Excess sodium in the soil limits the uptake of water due to decreased water potential, which may result in wilting; similar concentrations in the cytoplasm can lead to enzyme inhibition, which in turn causes necrosis and chlorosis (Zhu, 2001). To avoid these problems, plants developed mechanisms that limit sodium uptake by roots, store them in cell vacuoles, and control them over long distances; excess sodium may also be stored in old plant tissue, limiting the damage to new growth.

Salinity limits plant growth and impairs agricultural productivity (Eduardo et al., 2000). There is a wide spectrum of plant responses to salinity that are defined by a range of adaptations at the cellular and the whole-plant levels, however, the mechanisms of sodium transport appear to be fundamentally similar. At the cellular level, sodium ions gain entry via several plasma membrane channels. As cytoplasmic sodium is toxic above threshold levels, it is extruded by plasma membrane Na^+/H^+ antiports that are energized by the proton gradient generated by the plasma membrane ATPase. Cytoplasmic Na^+ may also be compartmentalized by vacuolar Na^+/H^+ antiports. These transporters are energized by the

proton gradient generated by the vacuolar H^+ -ATPase and H^+ -PPIase. Here, the mechanisms of sodium entry, extrusion, and compartmentation are reviewed, with a discussion of recent progress on the cloning and characterization, directly in plants and in yeast, of some of the proteins involved in sodium transport.

For agricultural plants, sensitivity to salinity is commonly (but not exclusively) due to the abundance of Na^+ in the soil as excess Na^+ is toxic to plants (Zhang et al., 2010). They considered reducing Na^+ uptake to be the key, as well as the most efficient approach, to control Na^+ accumulation in crop plants and hence to improve their salt resistance. Understanding the mechanism of Na^+ uptake by the roots of higher plants is crucial for manipulating salt resistance. Hence, the aim of this review is to highlight and discuss recent advances in our understanding of the mechanisms of Na^+ uptake by plant roots at both physiological and molecular levels. They concluded that continued efforts to investigate the mechanisms of root Na^+ uptake in higher plants are necessary, especially that of low-affinity Na^+ uptake, as it is the means by which sodium enters into plants growing in saline soils.

Pan et al., (2016) discussed that *Atriplex canescens* (flowering saltbush) is a C4 perennial fodder shrub with excellent resistance to salinity. However, the mechanisms underlying the salt tolerance in *A. canescens* are poorly understood. In this study, 5-weeks-old *A. canescens* seedlings were treated with various concentrations of external NaCl (0–400 mM). The results showed that the growth of *A. canescens* seedlings was significantly stimulated by moderate salinity (100 mM NaCl) and unaffected by high salinity (200 or 400 mM NaCl). Furthermore, *A. canescens* seedlings showed higher photosynthetic capacity under NaCl treatments (except for 100 mM NaCl treatment) with significant increases in net photosynthetic rate and water use efficiency. Under saline conditions, the *A. canescens* seedlings accumulated more Na^+ in either plant tissues or salt bladders, and also retained relatively constant K^+ in leaf tissues and bladders by enhancing the selective transport capacity for K^+ over Na^+ (ST value) from stem to leaf and from leaf to bladder.

External NaCl treatments on *A. canescens* seedlings had no adverse impact on leaf relative water content, and this resulted from lower leaf osmotic potential under the salinity conditions. The contribution of Na^+ to the leaf osmotic potential (9s) was sharply enhanced from 2% in control plants to 49% in plants subjected to 400 mM NaCl. However, the contribution of K^+ to 9s showed a significant decrease from 34% (control) to 9% under 400 mM NaCl. Interestingly, concentrations of betaine and free proline showed significant increase in the leaves of *A. canescens* seedlings, these compatible solutes presented up to 12% of contribution to 9s under high salinity. These findings suggest that, under saline environments, *A. canescens* is able to enhance photosynthetic capacity, increase Na^+ accumulation in tissues and salt bladders, maintain

relative K^+ homeostasis in leaves, and use inorganic ions and compatible solutes for osmotic adjustment which may contribute to the improvement of water status in plant.

Research over the last two plus decades, facilitated by advances in molecular genetics and biotechnology, and with genetic model systems, has identified genes involved in salt acclimation or adaptation and linked these to critical mechanisms and processes (Hasegawa, 2013). A case in point is present understanding of critical transport determinants that facilitate intra- and intercellular Na^+ homeostasis of plants in saline environments predominated by NaCl. Pumps in the plasma membrane (H^+ -ATPase), and the tonoplast (H^+ -ATPase) and H^+ pyrophosphatases (AVP1) generate proton electrochemical gradients necessary to energize Na^+ efflux to the apoplast and influx into vacuoles, respectively. The plasma membrane Na^+/H^+ antiporter SOS1 is responsible for apoplastic efflux, and NHX type Na^+/H^+ antiporters for vacuolar and endosomal compartmentalization. Ca_2^{+ext} reduces passive intracellular Na^+ influx cells by decreasing Na^+ transport through high affinity K^+ uptake systems and what are presumed to be nonselective cation channels, and activating, through the SOS signal pathway, the SOS1 plasma membrane Na^+/H^+ antiporter. Moreover, there is greater understanding about how cellular transport systems functionally integrate to facilitate tissue and organismal Na^+ homeostasis. Notable in this process are HKT1 Na^+ transporters, which regulate Na^+ loading into the root xylem, limiting flux to and accumulation in the shoot. This review will summarize ion transport systems that facilitate plant Na^+ homeostasis. Halophyte and glycophyte salinity responses and transport determinant function are compared and contrasted. The potential of halophytes as genetic resources for unique alleles or loci of transport protein genes and transcriptional and post-transcriptional regulation of transport protein function are discussed in the context of crop salt tolerance.

Diana et al (2013) found that salinization of agricultural land is an increasing problem. Because of their high tolerance to salinity, *Salicornia spp.* could become models to study salt tolerance; they also represent promising saline crops. The salinity-growth response curve for *Salicornia dolichostachya* Moss was evaluated at 12 salt concentrations in a hydroponic study in a greenhouse and at 5 different seawater dilutions in an outside setting. Salt concentrations ranged between 0 mM and 500 mM NaCl (\approx seawater salinity). Plants were grown for six weeks and morphological and physiological adaptations in different tissues were evaluated. *S. dolichostachya* had its growth optimum at 300 mM NaCl in the root medium, independent of the basis on which growth was expressed. The relative growth rate (RGR) in the greenhouse experiment was comparable with RGR-values in the outdoor growth experiment. Leaf succulence and stem diameter had the highest values at the growth optimum (300 mM NaCl).

Carbon isotope discrimination ($\delta^{13}C$) decreased upon salinity. *S. dolichostachya* maintained a lower leaf sap osmotic potential relative to the external solution over the entire salinity range, this was mainly accomplished by accumulation of Na^+ and Cl^- . Glycine betaine concentrations did not significantly differ between the treatments. $Na^+:K^+$ -ratio and K^+ -selectivity in the shoots increased with increasing salinity, both showed variation between expanding and expanded shoot tissue. We conclude that *S. dolichostachya* was highly salt tolerant and showed salt requirement for optimal growth. Future growth experiments should be done under standardized conditions and more work at the tissue and cellular level needs to be done to identify the underlying mechanisms of salt tolerance.

Adolf et al (2013) stated that In the face of diminishing fresh water resources and increasing soil salinisation it is relevant to evaluate the potential of halophytic plant species to be cultivated in arid and semi-arid regions, where the productivity of most crop plants is markedly affected. Quinoa is a facultative halophytic plant species with the most tolerant varieties being able to cope with salinity levels as high as those present in sea water. This characteristic has aroused the interest in the species, and a number of studies have been performed with the aim of elucidating the mechanisms used by quinoa in order to cope with high salt levels in the soil at various stages of plant development. In quinoa key traits seem to be an efficient control of Na^+ sequestration in leaf vacuoles, xylem Na^+ loading, higher ROS tolerance, better K^+ retention, and an efficient control over stomatal development and aperture. The purpose of this review is to give an overview on the existing knowledge of the salt tolerance of quinoa, to discuss the potential of quinoa for cultivation in salt-affected regions and as a basis for further research in the field of plant salt tolerance.

Sodium uptake from the soil is a major cause of salinity toxicity in plants, yet little is known about the mechanisms that underlie Na influx (Maathuis et al., 2001). They have characterized voltage independent channels (VICs) in Arabidopsis roots that are thought to contribute to Na entry. VICs showed no selectivity among monovalent cations, and their gating was found to be voltage independent. However, VIC open probability showed sensitivity to cyclic nucleotides. The presence of micromolar concentrations of cAMP or cGMP at the cytoplasmic side of the plasma membrane evoked a rapid decrease in channel open probability. In accord with predictions from electrophysiological data, these results showed that short-term unidirectional Na influx is also reduced in the presence of cyclic nucleotides. Moreover, addition of membrane permeable cyclic nucleotides during growth assays improved plant salinity tolerance, which corresponded with lower levels of Na accumulation in plants. These data implied that Arabidopsis plants may contain a cyclic nucleotide-based signaling pathway that directly affects Na transport via VICs.

Munns et al., (1986) observed that Na^+ transport in plants has largely been studied in the context of salinity stress or tolerance responses. Although there are some plants for which there is a growth requirement for Na^+ , particularly halophytes, there is little biological relevance in the study of Na^+ as a limiting micronutrient because it is an abundant element in soils and soil-solutions. Rather, an overabundance of sodium is a limiting factor to plant growth over large terrestrial areas of the world. The detrimental effect of salt on plants is the result of a combination of factors and can be observed at the whole-plant level as a decrease in growth rate, leaf damage, and an increase in root/shoot ratio. Moreover, the variability of plant growth responses to salinity defines a wide spectrum of salinity tolerance from the salt-sensitive glycophytes to the salt-tolerant halophytes. The strategies for maintaining a high K^+/Na^+ ratio in the cytosol include sodium extrusion and/or sodium compartmentation. The entry of Na^+ into the plant cell is essentially a passive process: the negative electrical potential difference at the plasma membrane and low cytosolic Na^+ concentrations strongly favor the movement of Na^+ into the cell. In contrast, Na^+ extrusion and compartmentation are, although indirectly, active processes. Na^+/H^+ antiporters mediate the compartmentation of Na^+ within the vacuole and the extrusion of Na^+ from the cell. These are two key processes in the concerted action of cytosolic Na^+ detoxification and cellular osmotic adjustment that are necessary to tolerate salinity stress.

K^+ in plant shoot, leaf and root

Maintaining constant intracellular ion homeostasis, especially K^+ and NaCl homeostasis, is essential for a series of physiological processes in living cells, and is more crucial for plant adapting to saline environments (Zhu, 2003; Tang et al., 2015; Glenn et al., 1996). To reduce cytosolic NaCl concentration, some halophytes developed a mechanism of ion compartmentation by sequestering excessive cytosolic NaCl into the central vacuole, which all alleviates the NaCl toxicity, thus maintains ion homeostasis and OA of cell in saline conditions (Zhu, 2003; Flowers et al., 2015). Swan, (1971) Unlike other major elements, potassium does not enter into the composition of any of the important plant constituents involved in metabolism, but it does occur in all parts of plants in substantial amounts. It seems to be of particular importance in leaves and at growing points. Potassium is outstanding among the nutrient elements for its mobility and solubility within plant tissues. Processes involving potassium include the formation of carbohydrates and proteins, the regulation of internal plant moisture, as a catalyst and condensing agent of complex substances, as an accelerator of enzyme action, and as contributor to photosynthesis, especially under low light intensity.

Sato et al., (1951) described that when soil-potassium levels are high, plants take up more potassium than needed for healthy growth. The

term luxury consumption has been applied to this. When potassium is moderately deficient, the effects first appear in the older tissues, and from there progress towards the growing points. Acute deficiency severely affects growing points, and die-back commonly occurs. Symptoms of potassium deficiency in white spruce include: browning and death of needles (chlorosis); reduced growth in height and diameter; impaired retention of needles; and reduced needle length (Heiberg et al, 1951). A relationship between potassium nutrition and cold resistance has been found in several tree species, including two species of spruce.

Potassium regulates the opening and closing of the stomata by a potassium ion pump (Munns et al., 1986). Since stomata are important in water regulation, potassium regulates water loss from the leaves and increases drought tolerance. Potassium deficiency may cause necrosis or interveinal chlorosis. The potassium ion (K^+) is highly mobile and can aid in balancing the anion (negative) charges within the plant. Potassium helps in fruit coloration, shape and also increases its brix. Hence, quality fruits are produced in potassium-rich soils. Potassium serves as an activator of enzymes used in photosynthesis and respiration. Potassium is used to build cellulose and aids in photosynthesis by the formation of a chlorophyll precursor. Potassium deficiency may result in higher risk of pathogens, wilting, chlorosis, brown spotting, and higher chances of damage from frost and heat.

Cl^- in the plant shoot, leaf and root

A cytosolically-directed electrochemical potential difference for Na^+ is also normally present across the vacuolar membrane. Such measurements as have been made (all on NaCl -stressed tissue) suggest that $[\text{Na}^+]$ is usually 2 to 8 fold higher in the vacuolar lumen than in the cytoplasm (Apse et al., 1999; Apse et al., 2003; Binzel et al., 1988; Hajibagheri et al., 1987). The compartmentation of Na^+ into the vacuoles provides an efficient mechanism to avert the toxic effects of Na^+ in the cytosol. Moreover, the compartmentation of Na^+ and Cl^- into the vacuole allows plants to use NaCl as an osmoticum to maintain an osmotic potential that drives water into the cells. The transport of Na^+ into the vacuoles is mediated by a Na^+/H^+ antiporter that is driven by the electrochemical gradient of protons generated by the V-type H^+ -ATPase and the H^+ -PPiase (Apse et al., 2003; Bao et al., 2008; Barkla et al., 1995; Blumwald et al., 2000; Gaxiola et al. 2001; He et al. 2005; Li et al., 2007, 2008; Yamaguchi and Blumwald 2005; Zhang and Blumwald 2001).

Conclusion

The potassium ion (K^+) is highly mobile and can aid in balancing the anion (negative) charges within the plant. Potassium helps in fruit coloration, shape and also increases its brix. Hence, quality fruits are produced in potassium-rich soils. Potassium serves as an activator of enzymes used in photosynthesis and respiration. The transport of Na^+ into the

vacuoles is mediated by a Na^+/H^+ antiporter that are driven by the electrochemical gradient of protons generated by the V-type H^+ -ATPase and the H^+ -Ppiase. The compartmentation of Na^+ and Cl^- into the vacuole allows plants to use NaCl as an osmoticum to maintain an osmotic potential that drives water into the cells.

References

- Adolf, V. I., Jacobsena, S. E., & Shabala, S. (2013). Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). *Environ. Exp. Bot.* 92, 43–54.
- Apse, M. P., Aharon, G. S., Snedden, W. A., & Blumwald, E. (1999). Salt tolerance conferred by over expression of a vacuolar Na^+/H^+ antiport in Arabidopsis. *Sci.* 285, 1256–1258.
- Apse, M. P., Sottosanto, J. B., & Blumwald, E. (2003). Vacuolar cation/ H^+ exchange, ion homeostasis, and leaf development are altered in a T-DNA insertional mutant of *AtNHX1*, the Arabidopsis vacuolar Na^+/H^+ antiporter. *Plant J.* 36, 229–239.
- Bao, A. K., Wang, S. M., Wu, G. Q., Xi, J. J., Zhang, J. L., & Wang, C. M. (2008). Over expression of the Arabidopsis H^+ -Ppiase enhanced the salt and drought tolerance in transgenic alfalfa (*Medicago sativa* L.). *Plant Sci.* 176, 232–240.
- Barkla, B. J., Zingarelli, L., Blumwald, E., & Smith, J. A. C. (1995). Tonoplast Na^+/H^+ antiport activity and its energization by the vacuolar H^+ -ATPase in the halophytic plant *Mesembryanthemum crystallinum* L. *Plant Physiol.* 109, 549–556.
- Binzel, M., Hess, F. D., Bressan, R. A., & Hasega, P. M. (1988). Intracellular compartmentation of ion in salt adapted tobacco cells. *Plant Physiol.* 86, 607–614.
- Blumwald, E. (2003). Engineering salt tolerance in plants. In: *Biotechnology & Genetic Engineering Reviews*, Vol 20, pp 261–275. Intercept Ltd. Scientific Technical & Medical Publishers.
- Blumwald, E., Aharon, G. S., & Apse, M. P. (2000). Sodium transport in plant cells. *Biochim Biophys Acta-Biomembr.* 1465, 140–151.
- Diana, K., Broekman, R., Rozema, J. (2013). Salt tolerance in the halophyte *Salicornia dolichostachya* Moss: Growth, morphology and physiology. *Environ. Exp. Bot.* 92, 32–4.
- Eduardo, B., Aharon, G. S., & Apse, M. P. (2000). Sodium transport in plant cells. *Biochimica et Biophysica Acta (BBA) - Biomembranes.* 1465, 1–2, 140–151. [http://dx.doi.org/10.1016/S0005-2736\(00\)00135-8](http://dx.doi.org/10.1016/S0005-2736(00)00135-8)
- Flowers, T. J., Munns, R., & Colmer, T. D. (2015). Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. *Ann. Bot.* 115, 419–431. doi: 10.1093/aob/mcu217
- Gaxiola, R. A., Li, J. S., Undurraga, S., Dang, L. M., Allen, G. J., Alper, S. L., & Fink, G. R. (2001). Drought- and salt-tolerant plants result from over expression of the AVP1 H^+ -pump. *Proc. Natl. Acad. Sci. USA* 98, 11444–11449.
- Glenn, E., Pfister, R., Brown, J. J., Thompson, T. L., & O'Leary, J. (1996). Na and K accumulation and salt tolerance of *Atriplex canescens* (Chenopodiaceae) genotypes. *Am. J. Bot.* 83, 997–1005.
- Hajibagheri, M. A., Harvey, D. M. R., & Flowers, T. J. (1987). Quantitative ion distribution within root cells of salt-sensitive and salt tolerant maize varieties. *New Phytol.* 105, 367–379.
- Hasegawa, P. M. (2013). Sodium (Na^+) homeostasis and salt tolerance of plants. *Environ. Exp. Bot.* 92, 19–31.
- He, C. X., Yan, J. Q., Shen, G. X., Fu, L. H., Holaday, A. S., Auld, D., Blumwald, E., & Zhang, H. (2005). Expression of an arabidopsis vacuolar sodium/proton antiporter gene in cotton improves photosynthetic performance under salt conditions and increases fiber yield in the field. *Plant Cell Physiol.* 46, 1848–1854.
- Heiberg, S. O., & White, D. P. (1951). Potassium deficiency of reforested pine and spruce stands in northern New York. *Soil Sci. Soc. Amer. Proc.* 15, 369–376.
- Kering, M. K. (2008). Manganese nutrition and photosynthesis in NAD-malic enzyme C4 plants. Ph.D. Dissertation. University of Missouri-Columbia. Retrieved 2011-11-09.
- Li, J., He, X., Xu, L., Zhou, J., Wu, P., Shou, H., & Zhang, F. (2008). Molecular and functional comparisons of the vacuolar Na^+/H^+ exchangers originated from glycophytic and halophytic species. *J. Zhejiang Univ. Sci. B* 9, 132–140.
- Li, J. Y., Jiang, G. Q., Huang, P., Ma, J., & Zhang, F. C. (2007). Overexpression of the Na^+/H^+ antiporter gene from *Suaeda salsa* confers cold and salt tolerance to transgenic *Arabidopsis thaliana*. *Plant Cell Tiss. Organ Cult.* 90, 41–48.
- Maathuis, F. J., & Sanders, D. (2001). Sodium uptake in Arabidopsis roots is regulated by cyclic nucleotides. *Plant Physiol.* 127, 1617–1625. doi:10.1104/pp.010502.
- Munns, R., & Termatt, A. (1986). Whole-plant responses to salinity. *Aust. J. Plant Physiol.* 13, 143–160.
- Pan, Y.-Q., Guo, H., Wang, S.-M., Zhao, B., Zhang, J.-L., Ma, Q., Yin, H.-J., & Bao, A.-K. (2016). The photosynthesis, Na^+/K^+ , homeostasis and osmotic adjustment of *Atriplex canescens* in response to salinity. *Front. Plant Sci.* 7, 848. doi: 10.3389/fpls.2016.00848
- Sato, Y., & Muto, K. (1951). Factors affecting cold resistance of tree seedlings. II. On the effect of potassium salts. *Hokkaido Univ. Coll. Agric. Coll. Exp. Forests, Res. Bull.* 15, 81–96.
- Subbarao, G. V., Ito, O., Berry, W. L., & Wheeler, R. M. (2003). Sodium—A functional plant nutrient. *Crit. Rev. Plant Sci.* 22, 5, 391–416. doi:10.1080/07352680390243495.
- Swan, H. S. D. (1971). Relationships between nutrient supply, growth and nutrient concentrations in the foliage of white and red spruce. *Pulp Pap. Res. Inst. Can., Woodlands Pap. WR/34.* 27 p.
- Tang, X. L., Mu, X. M., Shao, H. B., Wang, H. Y., & Brestic, M. (2015). Global plant-responding mechanisms to salt stress: physiological and molecular levels and implications in biotechnology. *Crit. Rev. Biotechnol.* 35, 425–437. doi: 10.3109/07388551.2014.889080
- Yamaguchi, T., & Blumwald, E. (2005). Developing salt-tolerant crop plants: challenges and opportunities. *Trends Plant Sci.* 10, 615–620.
- Zhang, H. X., & Blumwald, E. (2001). Transgenic salt tolerant tomato plant accumulate salt in the foliage not in the fruit. *Nat Biotechnol.* 19, 765–768.
- Zhang, J. L., Flowers, T. J., & Suo-Min, W. (2010). Mechanisms of sodium uptake by roots of higher plants. *Plant Soil* 326, 45–60. DOI 10.1007/s11104-009-0076-0
- Zhu, J. K. (2001). Plant salt tolerance. *Trends in Plant Sci.* 6, 2, 66–71. doi:10.1016/S1360-1385(00)01838-0. PMID 11173290.
- Zhu, J. K. (2003). Regulation of ion homeostasis under salt stress. *Curr. Opin. Plant Biol.* 6, 441–445. doi:10.1016/S1369-5266(03)00085-2