Chapter 11
Physiological and Molecular Responses to Salinity Due to Excessive Na^+ in Plants

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1 Introduction

Salinity is a crucial abiotic stress condition that hinders the growth and production of any crop (Long et al. 2020), particularly in arid and semi-arid regions (Munns and Tester 2008). This problem is relatively becoming higher due to problems of climate change, especially global warming. Misra et al. (2020b) had revealed that contribution of such soils in the world is 7%, having increased salt content and difficulty in leaching out of water (Zhao et al. 2007). Agricultural lands covering large areas under this abiotic stress cause heavy losses in economy of the world (Chaitanya et al. 2014). In India, saline soils cover a total area of about 6.73 million ha (of five states, Gujarat, U.P., West Bengal, Maharashtra and Rajasthan). Gujarat covers the highest area (2.23 million ha) of saline soil followed by U.P. (1.37 million ha), Maharashtra, West Bengal and Rajasthan (Sharma and Singh 2015). Sharma et al. (2014) had revealed that approximately 75% of soil in India belongs to saline (40%) and sodic (60%) categories. This amount is expected to increase thrice its present value to 20 million ha by the upcoming year 2050 (Sharma et al. 2014). The abiotic

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A. Husen (ed.), *Harsh Environment and Plant Resilience*,
https://doi.org/10.1007/978-3-030-65912-7_11

stresses prevent the plants to explore out their fully inherited potential of high yielding, leading to less crop yield (Cramer et al. 2011; Misra et al. 2020a; Ansari and Silva da 2012; Jalil and Ansari 2018; Jalil and Ansari 2020b). Amongst these abiotic stresses, salinity is a serious issue which is increasing day by day (Rogers and McCarty 2000). Saline soil can be defined as the one comprising of chloride and sulphates of four ions, viz., sodium, calcium, magnesium and potassium (Rani et al. 2019). There are many causes of elevation of sodium ions in soils. They are as follows: natural means through weathering of parental rocks (Szabolcs 1998), salt deposition in marine through wind and rains, anthropogenic activities, i.e. use of poor-quality war for irrigation of crops, global warming, etc. According to tolerance or sensitivity, plants are also grouped into glycophytes and halophytes. Zakharin and Panichkin (2009) had revealed that glycophytes are the ones which are sensitive towards salt-stress condition and majority of plants belong to this category. These plants even have slower growth rate when salt concentration in soil exceeds 0.01% (Dajic 2006). Regarding halophytes, these plants are bestowed with natural ability of tolerating high salt content, i.e. greater than 300–400 mmol NaCl (Cheeseman 2015).

In certain cases, salt stress also occurs in combination with other stresses creating a secondary salinity. Salt stress along with waterlogging is one amongst them which is becoming a crucial problem in Indian soils, chiefly in north western states (Singh et al. 2010). The losses caused due to these have resulted in monetary losses of Rs. 1669 million in Haryana (Datta and De Jong 2002). Munns and Tester (2008) had even showed that combination of nutrient imbalance and salt stress causes strong impact on photosynthesis resulting in chlorosis of plants. Parvaiz and Satyavati (2008) had shown that leaf senescence is another aspect which limits plant growth. Studies had reported that cotton plants exposed to salt-stress condition have poor growth germination and reduced seed yield. Furthermore, the quality of fibre of such plants is also low (Dong et al. 2009; Higbie et al. 2010). At times, salt stress even causes death of plants and it is known that plant growth is negatively affected when the range of salt stress lies from 0.2% to 0.5% (Yu et al. 2012). Considering the increasing problem of salt stress and its negative influence on plant growth, this chapter will highlight the physiological response in plants due to high accumulation of sodium ions as well as the response of various genes at molecular level under such a situation.

2 Physiological Response Under Increased Sodium Ions in Plants

When salt levels in soil get increased, it reduces plant water uptake (Maser et al. 2002). Once root uptakes a large amount of sodium and chloride ions from soil, the photosynthetic rate is declined and metabolic processes undergo alterations resulting in harmful effect on plant growth, irrespective of the growth stage (Maser et al.

2002). Plants exposed to high salt concentration undergo many alterations in physiological processes and are explained below.

1. *Photosynthesis Rate and Water Potential*: Photosynthesis is considered as a sensitive physiological aspect when sodium ions are excessive in plants. High amount of sodium ions in plants results in damage of photosynthetic apparatus due to dehydration of cell membrane resulting in closure of stomata. This in turn causes reduction in CO_2 permeability (Piotr and Giles 2009). Munns et al. (2006) had revealed that metabolic hindrance also occurs during photosynthesis in leaves when sodium ions are present in large amount in plants. Besides, when plants adapt to salt-stress condition, at times it changes its photosynthetic cycle which requires water for opening of stomata during night (Zhu and Meinzer 1999).
2. *Ionic Homeostasis and Compartmentalization*: In such a condition, sodium ion is transported from cytoplasm to vacuolar region via sodium hydrogen antiporter. Vacuolar type H^+-ATPase (V-ATPase), a type of H^+ pump, helps in regulating ion homeostasis and compartmentalization as well as its survival under salt-stress condition (Polash and Hossain 2019). Otoch et al. (2001) had revealed that V-ATPase activity is enhanced while vacuolar pyrophosphatase (V-PPase) activity is suppressed in cowpea hypocotyls under high sodium ions condition.
3. *Solute Accumulation*: Solute biosynthesis and accumulation get increased under salt-stress condition. Glycinebetaine, proline, trehalose, sugars, etc., are the solutes which are known to enhance their production and accumulation when sodium ions concentration gets increased (Ashraf and Foolad 2007; Tahir et al. 2012; Kerepesi and Galiba 2000). These solutes do not hinder with reactions occurring under normal condition (Hasegawa et al. 2000; Zhifang and Loescher 2003). Increased proline content under salt-stress condition is known to be seen in plants like sugar beet, *Brassica juncea*, tolerant sugarcane variety, etc. (Ghoulam et al. 2002; Yusuf et al. 2008; Vasantha and Rajlakshmi 2009). Biosynthesis and accrual of these solutes cause protective shield for the plant cells exposed to such a situation and help in maintaining the osmotic balance through incessant water supply (Hasegawa 2013).
4. *Enzyme Activity*: Inhibition in enzyme activity takes place when plants are exposed to salt-stress condition. Booth and Beardall (1991) had reported that the ratio of sodium to potassium is increased under salt-stress condition which results in inactivity of enzyme. This in turn causes changes in cellular metabolism and interruption in uptake of potassium ions. Furthermore, partition in the cells is also affected. On an overall basis, salt-stress condition causes an influence on opening of stomata due to which there is reduction in plant growth (Nawaz et al. 2010). Protein synthesis in such plants is also affected that results in reduction in leaf growth or at times may causes death of leaf (Ashraf 2004; Munns 2005).
5. *Ionic Balance*: Due to the excessive sodium ions in the root region of the plant, interruption in water uptake and nutrients is seen. This also contributes to alteration in plant metabolism (Munns 2002; Lacerda et al. 2003). Nutrient imbalance (due to higher Na^+, Cl^- ions accumulation) and deficiencies (due to interruption

in uptake of K+, Mn^{2+} ions, etc.) have been reported in plants exposed to salt-stress conditions (Karimi et al. 2005).

6. *Hormonal Balance*: Plants exposed to salt-stress condition have an imbalance of hormones due to reduction in osmotic potential (Khan and Weber 2008), changes in metabolism of nucleic acid, proteins and enzyme activity (Gomes-Filho et al. 2008; Yupsanis et al. 1994; Dantas et al. 2007).
7. *Nutrient Balance*: Under salt-stress condition, plants show an imbalance in nutrients. Several studies had shown that there was a decrease in uptake of nutrients along with its accumulation in salt-stress condition (Hu and Schmidhalter 2005; Jalil and Ansari 2019). This may even lead to nutrient deficiency or disorder at times in plants (Khorsandi and Anagholi 2009). Association of nutrient uptake and nutrients accumulation has been reported to be hampered under salt-stress condition because of two reasons, one being the composition of soil and other being the competition between various salts occurring due to sodium accumulation under salt-stress condition (Khorsandi and Anagholi 2009). There is also a reduction in accumulation of nitrogen under increased sodium ions due to Na^+ and NH_4^+ interaction and/or between NO_3^- and Cl^-. This results in reduction in yield and in plants like sugarcane, growth of the plant also gets influenced by salt stress (Rozeff 1995). Further, another nutrient, phosphorus is also revealed to be deficit in saline soils. This is so as activity of phosphate ion gets decreased. Epstein (1983) had shown that reduction in potassium, magnesium and calcium ions are seen in plants exposed to salt-stress condition which causes imbalance of nutrients. Furthermore, deficiency in micronutrients is also seen due to high pH values (Zhu et al. 2004). Chaitanya et al. (2014) had revealed that increase in sodium ions due to salt stress causes induction of potassium deficiency as plants selectively absorb these ions in comparison to sodium ions.
8. *Other Parameters*: When sodium and chloride ions are high, osmotic potential in soil is reduced which in turns results in water absorption by plant roots (Isayenkov 2012). Furthermore, increase in respiration rate and increase in ion toxicity are also observed in plants grown under salt stress. Besides, calcium displacement by sodium ions and permeability property of membrane cause membrane instability in plants of such condition.

3 Salt Overly-Sensitive (SOS) Stress-Signalling Pathway

Under salt-stress conditions, studies showed that salt overly-sensitive stress signalling is important for ion homeostasis as well as providing tolerance towards salt. There are basically three major proteins, viz., SOS 1, SOS 2 and SOS 3, involved in this signalling pathway that perform different functions. SOS 1 protein is responsible for controlling efflux of sodium ions at cellular level and long length of transportation from roots to shoot. It encodes Na^+/H^+ antiporter of plasma membrane.

Furthermore, this protein is reported to provide salt tolerance, if over-expressed in plants (Shi et al. 2002). SOS 2 protein consists of two terminal domains, N terminal which is the catalytic domain and C terminal which is the regulatory domain. This protein is known to encode serine/threonine kinase and is activated by combination of SOS 3 protein and Ca^{2+} ions (Liu et al. 2000). SOS 3 protein is also referred to as myristoylated Ca^{2+} binding protein. This protein has myristoylation site at its N-terminus, known to play important role in providing tolerance against salt stress (Ishitani et al. 2000).

The SOS signalling pathway is depicted in Figure 1, which illustrates that SOS signalling gets activated when SOS 2 protein (particularly regulatory domain of C terminus) initiates kinase by interacting with calcium-binding ions of SOS 3 proteins (Guo et al. 2004) after which phosphorylation of SOS 1 protein occurs due to the activated kinase which increases the activity of transportation of ions through Na^{+}/H^{+} antiporter (Quintero et al. 2002). Martinez-Atienza et al. (2007) had revealed that this rise causes efflux of sodium ions into the cells making sodium ion toxicity ease out (Fig. 11.1).

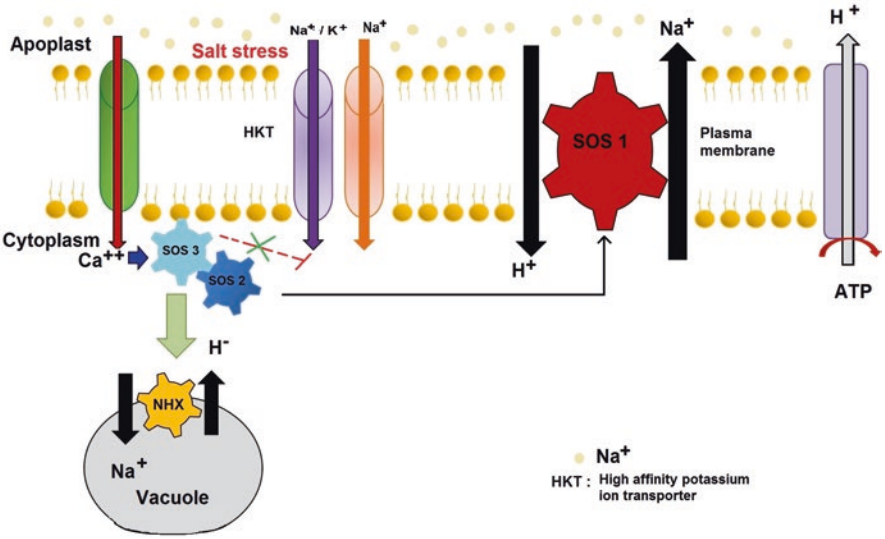

Fig. 11.1 SOS pathway model in plants exposed to salt stress. Under salt-stress condition, when sodium ions are high at plasma membrane, it induces calcium ion influx. On influx of calcium ions, SOS 3 gene alters its conformation and thereafter interacts with SOS 2 for its auto-inhibition. SOS 2 in complex with SOS 3 phoshorylates SOS 1. The complex of SOS 3 and SOS 2 inhibits HKT1 activity while SOS 2 activates activity of NHX. This in turn causes Na+/H+ antiporter to get activated for efflux of excess sodium ions

4 Halophytes: Tolerance Capability Under Increased Sodium Ions

Halophytes are the plants which have the property to survive under such saline environment and this salt increase helps in their growth and development. In *Suaeda salsa*, role of V-PPase is not much in salt environment while V-ATPase activity is upregulated. Halophytes are known to tolerate excessive sodium chloride ions either by salt-tolerant mechanism or by salt-avoidance mechanism. In salt-tolerance mechanism adopted by halophytes, studies have illustrated that reduction of sodium ion influx, excretion of sodium ions and compartmentalization are the three strategies involved (Flowers and Colmer 2015; Misra et al. 2020b) while in salt avoidance, strategies involved are shedding, secretion and succulence (Aslam et al. 2011; Shabala et al. 2014). Another way of halophyte to survive under saline environment is sequestration of salts into cell vacuoles which occurs via transporters. These transporters help in maintaining the ratio of potassium and sodium ions in cytosol (Kronzucker and Britto 2011; Sreeshan et al. 2014). High production of osmolytes such as proline, polyphenols, etc., also acts as osmo-protectants in halophytes which provides the capacity to tolerate such condition (Lokhande and Suprasanna 2012; Patel et al. 2016). In respect to genes imparting tolerance to such condition, halophytes regulate through mechanism of ABA dependent or ABA independent. There are two ways by which halophytes survive under such condition. They are as follows:

1. *Salt-Avoidance Mechanism*: In halophytes, salt-secreting structures such as salt hairs or salt glands are present. In certain halophytes, excess salt is secreted in liquid form which takes crystal formation when it comes under contact of air. These crystals appear on leaves of the plant. Balsamo et al. (1995) had reported that these crystals are washed off during heavy rains or in tides, thus, preventing the reabsorption of it into the cells of leaves. In shredding strategy, older leaves of the plants are shredded so as to avoid toxicity of salt (Mishra and Tanna 2017). Several studies had reported this method of mechanism for tolerance adaption in halophytes (Rozema et al. 1981; Waisel et al. 1986; Shabala et al. 2014).
2. *Salt-Tolerant Mechanism*: In plants several physiological aspects such as water status, transpiration, leaf area, antioxidant production, transpiration use efficiency, etc. contribute to tolerate salt stress (Ashraf 2009; Barbieri et al. 2012; Harris et al. 2010; Maggio et al. 2007). Munns and Tester (2008) had revealed that there are three mechanisms by which plants undergo salinity tolerance. These are: ion exclusion, tissue tolerance and shoot ion-independent tolerance. In ion exclusion, toxic ions from shoot are excluded out. In tissue tolerance, toxic ions are compartmentalized into particular tissues, cells and subcellular organelles. In shoot ion-independent tolerance, growth of the plant and water uptake by the plant is independent of the sodium ions accumulate under salt-stress condition (Fig. 11.2).

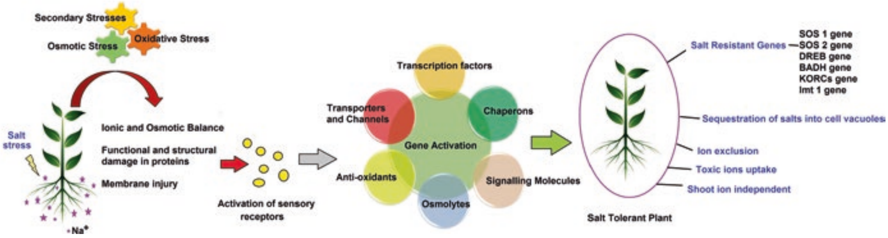

Fig. 11.2 Salt tolerant mechanism in halophytes under salt-stress condition

5 Molecular Response in Plant: Tolerance to Saline Environment Condition

Expression of many plant genes has been showed to regulate transcriptional and post-transcriptional process under salt-stress condition (Jalil and Ansari 2020a; Long et al. 2020). Understanding the molecular mechanism involved under such a condition is difficult as revealed by several studies (Munns and Tester 2008; Zhu 2001; Zhu 2002). The most important gene that plays a role under salt-stress condition is SOS 1 gene which is known to be upregulated (Oh et al. 2009; Shi et al. 2000). In certain plants like *Thellungiella*, genes associated with photosynthesis process do not show much changes under such condition (Wu et al. 2012); however, in plants like *Oryza sativa*, such genes play a role in recovering from stress (Zhou et al. 2009). Characterization of expression of genes and proteins under salt stress has also been reported in several plants like *Oryzae sativa, Nicotinum tobaccum, Medicago truncatula, Triticum aestivum,* and *Arabidopsis thaliana* (Sobhanian et al. 2010; Capriotti et al. 2014; Ghaffari et al. 2014). Heat shock proteins also play a role in plants exposed to salt-stress condition. Manaa et al. (2011) had revealed the upregulation of heat shock proteins in tomato plants exposed to salt-stress conditions. Long et al. (2020) had shown that heat shock protein (70 kDa) was upregulated in Zhongmu-1 (S28), but downregulated in Jemalong A17 (T26). Besides, Wu et al. (2012) had revealed that genes responsible for photosynthesis processes do not vary much under such a condition in plants which are tolerant to it like *Thellungiella,* whereas in rice, variation has been observed but it has been correlated with stress recovery (Zhou et al. 2009). Furthermore, Sewelam et al. (2014) had illustrated that there are many stress-responsive genes which are expressed due to combination of salt and osmotic stress, as ionic and osmotic stresses are the secondary stresses induced by excessive salt content. Salt stress solely generates 932 genes in *Arabidopsis* while 435 overlapping genes are expressed along with 367 repressive genes solely by salt stress and 154 overlapping genes (Sewelam et al. 2014).

Certain plants are also capable of tolerating salt stress. As a response to salt stress, high affinity potassium ion transporter 1 (HKT1) is an important determinant considered for such a condition. Studies had revealed that this gene helps in improving salt-tolerance capability as it lowers accumulation of sodium ions in tissue of shoot (Horie et al. 2009; Møller et al. 2009). In *Arabidopsis* plant, htk1 mutant expresses higher sodium ions in shoots while lesser in roots under salt-stress condition (Rus et al. 2004; Davenport et al. 2007). Møller et al. (2009) had also showed that HKT1 gene expressed in tissues of vascular bundle or pericycle are known to increase salt tolerance in plants. Furthermore, hkt1 mutations are known to suppress hypersensitive phenotypes associated with this stress (Rus et al. 2001; Rus et al. 2004). Studies had also revealed that HKT proteins are also important in plants as a response towards salt stress during developing new plant genotype through breeding (Asins et al. 2013; Ariyarathna et al. 2016). Yang and Guo (2018) had illustrated that there are other unidentified and SOS genes which are expressed in specific tissues under such condition for improving tolerance power against salt stress.

6 Conclusion

Salt stress is causing severe problems to agriculture and productivity. It is affecting physiological processes as well as alteration in osmotic and ionic balance has also been reported that leads to decline in biomass production. Salt stress does not affect the plant on a single growth stage rather it causes adverse effect on any plant growth stage at which it strikes. Salt stress also causes other secondary stress like osmotic stress leading to more severe impact on the plant growth. Several physiological responses have been known to cause alteration in plants, such as photosynthetic rate, hormone imbalance, and ionic imbalance. Since last two decades, salt-tolerance genes have also been identified using molecular approaches for coping with such condition. Genomic studies have also been reported in salt-tolerant plants. Identification and cloning of several genetic loci which are playing role in salt stress have been done. Transgenic plants are being developed for tolerating such situation and enhancing productivity under field conditions. In order to enhance tolerance towards this stress, it is vital to identify and characterize determinants and mechanism behind regulation of these determinants. There is a need to know molecular mechanism mediated by salt-responsive genes for regulating the developmental process of plant. Furthermore, there is a need to identify the markers for salt-tolerance capability for breeding programmes.

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