

Salt tolerance approaches in plants: Biotechnological perspective

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ABSTRACT

Climatic changes may affect soil quality of agricultural lands, especially by increasing salts deposition in the soil which results in soil salinity. Salinity stress affects several aspects of plant physiology, such as suppressing seed germination, reducing growth of roots and shoots, and altering growth regulators. Breeding salt tolerant plant cultivars has been proven inadequate to fully alleviate this problem. Salinity tolerance results from diverse mechanism, each controlled by a multi-gene system. Over the past decades, substantial progress has been made to elucidate the mechanisms underlying plant responses to mitigate adverse impacts of salinity. The overall problem is more tractable, if the plant response is dissected into diverse traits that are hypothesized to be involved in the tolerance to salinity. In this review, we comprehensively discuss plant adaption to salinity, the salt overly sensitive (SOS) pathway, ion homeostasis, determination of solutes and various molecular and proteomic approaches to understanding the salinity responses. This review provides response guidelines to enhance improvement of plant salt tolerance in combination with improved agricultural practices under saline conditions. Comprehensive understanding of all mechanisms for salinity stress response should be the ultimate of future studies.

Keywords: Salinity, ion homeostasis, transcriptional factors, salt overly sensitive pathway, proteomics.

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INTRODUCTION

Several types of abiotic environmental stresses are unfavorable for the plant growth and productivity. These abiotic stresses include drought, heat, salinity and alkalinity. Salt accumulation is one of the most important and common soil problems, especially in arid and semiarid regions, which have a negative impact on development and plant growth (Parvaiz and Satyawati, 2008). Normally, soil salinity can affect the plants in two different ways, *i.e.* higher salts concentration can hinder water intake through the roots, and can also affect the plant itself (Munns and Tester, 2008). Most plants are quite sensitive to environmental stresses, such as drought and salinity. However, plants can be divided into two major types on the basis of salinity tolerance, such as halophytes (can grow in saline conditions), and glycophytes (limited growth or early plant death under

salinity). The most important crops belong to the second category. In fact, crops belong to second category produced less yields under NaCl stress (Sadat Noori et al., 2011).

In this review, we discussed about three main categories such as; physiological; biochemical and molecular factors associated with salt tolerance mechanisms.

REVIEW

Plant adaptation to salinity (Background)

Some plants have ability to develop different defense mechanisms and able to adapt unfavorable situations

including salt stress (Fu et al., 2011). The reduction of plant productivity caused by the salinity stress involves physiological and metabolic processes depending on the level of exposure and duration of stress (James et al., 2011). Among major cereals barley (*Hordeum vulgare*) demonstrated highest degree of salt tolerance as compared to rice (*Oryza sativa*) and wheat (*Triticum aestivum*) (Deivanai et al., 2011; Ndimba et al., 2005). Salinity stress is a complicated factor in plant development especially in physiological classification, because plants integrate positive and negative-regulation under salinity. However, photosynthesis plays an important role with combination of organic solutes under salt stress treatment (Ashraf, 2004). Leaves of glycophytic plants cannot prevent a high level of salt damage, the study of Rawson et al. (1988) ensured that, compared to control treatments, NaCl stress reduced the overall area of all leaves gradually under 175 mol m^{-3} NaCl treatment, while the reduction was more than twice that in 100 mol m^{-3} NaCl. Table 1 represents a wide range of salinity from non-saline to very strong saline. Salinity of soil varies from spring to fall, and high concentrations of salts commonly appear on the surface of soil after spring thaw.

Ion homeostasis in salinity (physiological perspective)

Ion uptakes play a vital role in the growth process during salt stress. Plants uptake Na^+ and K^+ by their roots and transport them to other organs of plant. Previously working with sea aster (*Aster tripolium*) and ajwan (*Trachyspermum ammi*) found that the uptake of Na^+ and K^+ reduced root osmotic potential (Ashraf and Orooj, 2006; Ueda et al., 2003). Study by Wang et al. (2001) showed that, sea-blites (*Suaeda salsa*) growth under 0.1 M KCl was reduced by osmotic stress. Yokoi et al. (2002) explained different transport systems that facilitate cellular capacity to utilize Na^+ for osmotic adjustment in plant growth. The vacuolar sodium sequestration is mediated by secondary active Na^+ antiport and energized by a proton force which driven by vacuolar H^+ -ATPase under salinity stress in the halophytic plant (ice plant, *Mesembryanthemum crystallinum*). Every crop has different salinity tolerance mechanisms for example, barley (*Hordeum vulgare*) is superior to wheat and has more capability to accumulate high amount of Na^+ in its shoot (Roy et al., 2014). In accordance to this fact, some genes play a vital role in ion homeostasis in different plants such as HAL5 and AtNHX1 in *Arabidopsis thaliana*, TaSTRG in wheat (*Triticum aestivum*), (Table 2) under different salinity stress.

Determination of solutes (biochemical perspective)

Plants accumulate a variety of compatible osmolytes in

the cytosol, in order to decrease osmotic potential, maintain water uptake from saline soil solutions and limit salt absorption (Shahbaz and Ashraf, 2013). However, many plants contain organic osmolytes to tolerate osmotic stress. Under environmental stress the metabolism of plants is changed, e.g. different protein genes are induced in plant metabolism and investigation of these changes is necessary (Chinnusamy et al., 2005). Technologies like mass spectrometry (MS), Nuclear magnetic resonance spectroscopy (NMR), and Gas chromatography–mass spectrometry (GC-MS) can analyze a large number of small molecules (Kopka et al., 2004). Moreover, plants can also alter osmotic stress by accumulating high concentration of compatible solutes in the cytoplasm. Compatible solutes in the plant's cells include N-containing compounds (proline and glycine betaine), straight-chain polyhydric polyols (cyclic polyhydric alcohols, mannitol and sorbitol), and sugars (sucrose and raffinose). Recently, several researchers have reported the external application of metabolites, such vitamins (biotin and thiamine), amino acids (cysteine and methionine), and thioredoxin system (glutathione lipoic acid and glucosinolates) which can enhance the salinity tolerance in plants (Chen and Murata, 2002; Ashraf and Harris, 2013). At the end of last century, and with the help of genetic transformation new pathways for the biosynthesis of various compatible solutes into plants were established and produced transgenic plants with improved tolerance to stress (Nuccio et al., 1999). With the benefit of gene transformation technology many researchers modified different genes for enhancing the salt tolerance mechanism in different crops to cope with different salinity conditions. Some of these genes documented in (Table 2).

Molecular approaches in salinity (molecular perspectives)

Salinity tolerance is a polygenic process, which controls numerous physiological and biochemical functions at cellular, molecular and/or whole plant levels. The mechanism of salt tolerance at different stages of plant development is very complex (Ismail et al., 2014). The organization of molecular networks cascades is correlated to salt stress. Salt sensitivity; precise gene expression, metabolites, and signal transduction (from roots into cellular and total plant levels) are factors contributing to plant variation in environmental stress tolerance. The tolerance mechanism at molecular level is an essential regulator in breeding and genetic engineering to the salinity tolerance of crops. The salinity tolerance mechanism consists of key factors such as antioxidant defense system, ion homeostasis, buildup of compatible solutes and transcription factors (Chaitali and Sengupta, 2014). To increase the salt tolerance of plants, there is a need to consider the control mechanism at

Table 1. Salinity ranges according to soil depth.

Soil depth	Soil saline				
	Non	Weak	Moderate	Strong	Very Strong
0-60 cm (0-2 ft)	<2 mM NaCl	2-4 mM NaCl	4-8 mM NaCl	8-16 mM NaCl	>16 mM NaCl
60-120 cm (2-4 ft)	<4 mM NaCl	4-8 mM NaCl	8-16 mM NaCl	16-24 mM NaCl	>24 mM NaCl

Table 2. Compatible solutes (genes) enhanced tolerance stress in plants.

Gene name	Species	Enhanced tolerance	Reference
<i>mt1D</i>	Arabidopsis	Salt	Thomas et al. (1995)
<i>S6PDH</i>	Persimmon	Salt	Gao et al. (2001)
<i>imt1</i>	Tobacco	Salt	Sheveleva et al. (1997)
<i>PDH45</i>	Tobacco	Salt	Sanan-Mishra et al. (2005)
<i>PDH45</i>	Rice	Salt	Amin et al. (2012)
<i>PSP68</i>	Rice	Salt	Banu et al. (2015)
<i>AtHELPS</i>	Arabidopsis	Salt	Xu et al. (2011)
<i>PSP68</i>	Pea	Salt	Tuteja et al. (2015)
<i>PeJRL</i>	Arabidopsis	Salt	Zhang et al. (2019)
<i>SOS1</i>	Egg plant	Salt	Li et al. (2019)

molecular levels of plant development. Saline conditions lead to changes in the pattern of gene expression, qualitative and quantitative variation in the protein amalgamation. On the other hand, there is more common observation that salt stress obtains quantitative changes in the protein expressions. Comprehensive approach is really important to understand the molecular mechanism of salinity tolerance in different crops. With the help of transcription and proteomics technologies, we can approach and evaluate the molecular mechanisms of salt stress in plant (Roy et al., 2014; Shang et al., 2012).

Salt overly sensitive signaling

Salt overly sensitive (SOS) pathway has been demonstrated to play a key role in ion homeostasis and salt tolerance (Hasegawa, 2013). The SOS pathway consists of three types, *i.e.* SOS1, SOS2 (protein module is the Ser/Thr protein kinase), and SOS3 (calcium binding protein) as shown in Table 3. Among all the components of SOS pathway, SOS1 gene is considered particularly important and is responsible for encoding the gene for Na⁺/H⁺ transporter in plasma membrane. Moreover, phosphorylation of SOS3 and SOS2 complex leads to activation of SOS1 (Zhu, 2003). The newly activated pathway of SOS3-SOS2 has many effects and stimulates several genes and transcriptional factors of SOS1 and stabilizes cellular levels of SOS1 mRNA (Martínez et al., 2007). The phosphorylated form of SOS1 plays an essential role in Na^s efflux and contributes to the reduction of Na⁺ toxicity. Overall, SOS1 functions as an

Na⁺ transporter and mainly exists in the cytosolic compartment of the cell along with the Na⁺ sensor (Plett and Møller, 2010). SOS1 is expressed in all growing tissues and it is more active in the epidermal cells which are surrounded by the root tip and parenchyma cells bordering with the xylem. Moreover, SOS2 and SOS3 genes play important role in kinase activity and protein binding in plants during salinity, these SOS pathway genes are similar like other signal transduction pathways. The SOS2 and SOS3 supposed to facilitate the Na⁺/H⁺ antiport activity of SOS1 (Ji et al., 2013). This plasma membrane Na⁺/K⁺ antiporter controls Na⁺ efflux from the roots and transports these Na⁺ ions into the xylem, which are important for the regulation of Na⁺/K⁺ homeostasis, salt tolerance, and SOS1. The SOS pathway in salt stress generates Ca²⁺ signal which is mainly contributed by SOS3. Numerous investigations have shown that SOS3 can interface with SOS2. It may well operate between the SOS2-SOS1 interaction to reduce down extreme Na⁺ damage and support ion homeostasis (Tester and Davenport, 2003; Kim et al., 2007).

Transcriptional factors associated with salinity

Transcription factors are DNA binding protein activators and/or repressors for transcription of genes related to stress as shown in (Table 4). Physiological and biochemical alterations in salt-affected plant organs are accompanied by changes in transcriptional factors (Wei et al., 2000). Gene expression analysis of rice varieties differing in salt tolerance suggested that OsEREBP2

Table 3. Function of SOS family and ion homeostasis genes of salinity.

	Gene name	Species	Gene functions	Reference
SOS family genes	SOS1		Plasma membrane Na ⁺ /K ⁺ antiporter	Chakraborty et al. (2012)
	SOS2	<i>Brassica juncea</i>	Protein kinase	
	SOS3	<i>Brassica campestris</i>	Calcium-binding protein	
Genes involved in the ion homeostasis	HAL5		Regulate Na ⁺ /K ⁺ homeostasis	Lim et al. (2010)
	AtNHX1	<i>Arabidopsis thaliana</i>	vacuolar Na ⁺ /K ⁺ antiporter	Shang et al. (2012)
	TaSTRG	<i>Triticuma estivum</i>	Higher salt tolerance, Na ⁺ /K ⁺ ratio	Zhou et al. (2009)

Table 4. List of transcriptional factors.

Gene name	Species	Gene functions	Reference
AtSKIP	<i>Arabidopsis thaliana</i>	Transcription factor	Lim et al. (2010)
JcDREB	<i>Arabidopsis thaliana</i>	Transcription factor	Tang et al. (2011)
SNAC1	<i>Oryza sativa</i>	Transpiration rate	Liu et al. (2014)
ANAC092	Arabidopsis	Transcription factor	Balazadeh et al. (2010)
CaRAV1	Pepper	Transcription factor	Lee et al. (2010)
SNAC2	Rice	Transcription factor	Hu et al. (2008)
GmDREB1	Alfalfa	Transcription factor	Jin et al. (2010)
HD-Zip	Cotton	Transcription factor	Ni et al. (2008)
VvWRKY30	Grape	Transcription factor	Zhu et al. (2019)
NRAMP-2	Wheat	Transcription factor	Oyiga et al. (2019)

gene is involved in the salt stress. Similarly, bZIP class of ABRE binding transcription factor known as OSBZ8 has been identified in rice and showed high expression in salt tolerant cultivars as compared to salt sensitive ones (Serra et al., 2013). In *Arabidopsis thaliana* AtSKIP gene plays an important role in the transcription levels at 150 mM concentration of salt. JcDREB gene regulation was observed in *Arabidopsis thaliana* at 300 mM concentration of salinity. Seki et al. (2002) reported that, salinity induced 194 transcripts and these transcripts play important role in different proteins, which might be functioning in stress tolerance of *Arabidopsis thaliana*. In another study, the overexpression of SNAC1 transcript induced more tolerance to salt stress in cotton and reduced respiration rate. In agreement with above statements, we assume that, transcriptional factors play vital role during salinity treatments and improve the salt tolerance mechanism in plants (Liu et al., 2014).

Proteomic response to salinity

Developments in proteomic knowledge concerning protein separation and detection have an increasing impact on the study of plants responses to salinity stress. Proteomic studies for the analysis of salt tolerance were carried out in plant species such as *Arabidopsis*

(*Arabidopsis thaliana*), rice (*Oryza sativa*), barley (*Hordeum vulgare*), wheat (*T. aestivum*), tomato (*Solanum lycopersicum*) and tobacco (*Nicotiana tabacum*). Proteomics provides a potent method for studying secondary metabolism in plants and plant cells. In fact, during translation process, transcripts (mRNAs) converted to protein. Each mRNA corresponds to a specific amino acid sequence and forms the resultant proteins. So, many proteins play a dynamic role in plant stress tolerance, such as HSPs, LEAs, proteins involved in repair and protection from damages (Khan et al., 2007). The study of Moons et al. (1995) revealed that, the accumulation of proteins in two salt-tolerant rice genotypes, Pokkali and Nona Bokra under salt stress were significantly higher compared to control. The proteins which play an important role in salinity tolerance in different crops are presented in Table 5.

OVERALL CONCLUSION AND FUTURE PERSPECTIVES

Salinity is a substantial problematic issue all over the world and disturbing agricultural practices. It is predicted that after few years in future, salinity will become a bigger issue for farmers and researchers. In our review, we discussed salinity issue and tried to figure out the different aspects associated with salt tolerance

Table 5. Identified major proteins increased in crop plants under salt stress using proteomics.

Protein name	Species	Studies	Reference
<i>SaIT</i>	Rice	2-DE analysis for characterization of gene showing specific expression	Claes et al. (1990)
<i>OEE1</i>	Halophytes	Proteomic approach for the analysis of OEE1 protein in response to salt treatment in <i>Bruguiera gymnorhiza</i>	Sugihara et al. (2000)
26 kDa	Wheat	2-DE analysis of salt stress on peptide pattern	Majoul et al. (2000)
Tubulin α D	Rice	Proteomic analysis of salt stress response in seedlings of two African rice cultivars	Damaris et al. (2016)
MLP-like protein 328	canola	Proteomic analysis of salt-responsive proteins in canola roots by 2-DE and MALDI-TOF MS	Kholghi et al. (2019)
cpPDC	Sea purslane	Proteomic analyses of the chloroplasts <i>Sesuvium portulacastrum</i> under differential salt conditions	Peng et al. (2019)
OEE1	Rice	Mapping the 'early salinity response' triggered proteome adaptation in contrasting rice genotypes using iTRAQ approach	Lakra et al. (2019)
PS II 5 kDa p	Watermelon	iTRAQ-based quantitative proteomics analysis of cold stress-induced mechanisms in grafted watermelon seedlings	Shi et al. (2019)
PSB27	Narrow-leaved purple coneflower	Proteomics Analysis of <i>E. angustifolia</i> seedlings inoculated with Arbuscular Mycorrhizal Fungi under salt stress	Jia et al. (2019)
FBA	Rice	TRAQ-based protein profiling and biochemical analysis of two contrasting rice genotypes revealed their differential responses to salt stress	Hussain et al. (2019)

mechanisms. In the first section, we indicated important parameter of salt stress such as, ion homeostasis (the fundamental feature of salt stress). In second section, we focused on the biochemical aspects and emphasized about new technology for solutes analysis from salty plants and their genetic functions related to salt tolerance mechanisms. In our third section we discuss about molecular tactics to enlighten the salt stress problem and uses of different approaches to overcome these issues such as, salt signaling pathway, the genes/ transcripts interrelated with salinity in different plants, genetic functions linked with proteins accumulations with different experimental methodologies. In these scenarios, we concluded that traditional breeding approaches are not sufficient to overcome this issue. The breeders, scientists and researcher are needed to consider more about salinity issue. They should address more authentic experimental results, implementation of new technologies and genetic manipulation, transformation, and emphasis the new revaluations and most important subject is to develop salt-tolerant cultivars to cope with salinity issue.

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