

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⁺ 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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REFERENCES

- Amin M, Elias SM, Hossain A, Ferdousi A, Rahman MS, Tuteja N, Seraj ZI, 2012. Over-expression of a DEAD-box helicase, PDH45, confers both seedling and reproductive stage salinity tolerance to rice (*Oryza sativa* L.). *Mol Breed*, 30(1): 345-354.
- Ashraf M, 2004. Some important physiological selection criteria for salt tolerance in plants. *Flora-Morphol Distribut Functinal Ecol Plants*, 199(5): 361-376.
- Ashraf M, Harris P, 2013. Photosynthesis under stressful environments: an overview. *Photosynthetica*, 51(2): 163-190.

- Ashraf M, Orooj A, 2006.** Salt stress effects on growth, ion accumulation and seed oil concentration in an arid zone traditional medicinal plant ajwain (*Trachyspermum ammi* [L.] Sprague). *J Arid Environ*, 64(2): 209-220.
- Balazadeh S, Siddiqui H, Allu AD, Matallana-Ramirez LP, Caldana C, Mehrnia M, Zanor MI, Köhler B, Mueller-Roeber B, 2010.** A gene regulatory network controlled by the NAC transcription factor ANAC092/AtNAC2/ORE1 during salt - promoted senescence. *The Plant J*, 62(2): 250-264.
- Banu MSA, Huda KMK, Sahoo RK, Garg B, Tula S, Islam SS, Tuteja R, Tuteja N, 2015.** Pea p68 imparts salinity stress tolerance in rice by scavenging of ROS-mediated H₂O₂ and interacts with argonaute. *Plant Mol Biol Report*, 33(2): 221-238.
- Chaitali R, Sengupta D, 2014.** Effect of short term NaCl stress on cultivars of *S. lycopersicum*: a comparative biochemical approach. *J Stress Physiol Biochem*, 10(1): 59-81.
- Chakraborty K, Sairam RK, Bhattacharya R, 2012.** Differential expression of salt overly sensitive pathway genes determines salinity stress tolerance in Brassica genotypes. *Plant Physiol Biochem*, 51: 90-101.
- Chen TH, Murata N, 2002.** Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Curr Opin Plant Biol*, 5(3): 250-257.
- Chinnusamy V, Jagendorf A, Zhu JK, 2005.** Understanding and improving salt tolerance in plants. *Crop Sci*, 45(2): 437-448.
- Claes B, Dekeyser R, Villarroel R, Van den Bulcke M, Bauw G, Van Montagu M, Caplan A, 1990.** Characterization of a rice gene showing organ-specific expression in response to salt stress and drought. *Plant Cell*, 2(1): 19-27.
- Damaris RN, Li M, Liu Y, Chen X, Murage H, Yang P, 2016.** A proteomic analysis of salt stress response in seedlings of two African rice cultivars. *Biochimica et Biophysica Acta (BBA) - Proteins and Proteomics*, 1864(11): 1570-1578.
- Deivanai S, Xavier R, Vinod V, Timalata K, Lim O, 2011.** Role of exogenous proline in ameliorating salt stress at early stage in two rice cultivars. *J Stress Physiol Biochem*, 7(4): 157-174.
- Fu XZ, Khan EU, Hu SS, Fan QJ, Liu JH, 2011.** Overexpression of the betaine aldehyde dehydrogenase gene from *Atriplex hortensis* enhances salt tolerance in the transgenic trifoliolate orange (*Poncirus trifoliata* L. Raf.). *Environ Exper Bot*, 74: 106-113.
- Gao M, Tao R, Miura K, Dandekar AM, Sugiura A, 2001.** Transformation of Japanese persimmon (*Diospyros kaki* Thunb.) with apple cDNA encoding NADP-dependent sorbitol-6-phosphate dehydrogenase. *Plant Sci*, 160(5): 837-845.
- Hasegawa PM, 2013.** Sodium (Na⁺) homeostasis and salt tolerance of plants. *Environ Exper Bot*, 92: 19-31.
- Hu H, You J, Fang Y, Zhu X, Qi Z, Xiong L, 2008.** Characterization of transcription factor gene SNAC2 conferring cold and salt tolerance in rice. *Plant Mol Biol*, 67(1-2): 169-181.
- Hussain S, Zhu C, Bai Z, Huang J, Zhu L, Cao X, Nanda S, Hussain S, Riaz A, Liang Q, 2019.** iTRAQ-based protein profiling and biochemical analysis of two contrasting rice genotypes revealed their differential responses to salt stress. *Int J Mol Sci*, 20(3): 547.
- Ismail A, Takeda S, Nick P, 2014.** Life and death under salt stress: same players, different timing? *J Exper Bot*, 65(12): 2963-2979.
- James RA, Blake C, Byrt CS, Munns R, 2011.** Major genes for Na⁺ exclusion, Nax1 and Nax2 (wheat HKT1; 4 and HKT1; 5), decrease Na⁺ accumulation in bread wheat leaves under saline and waterlogged conditions. *J Exper Bot*, 62(8): 2939-2947.
- Ji H, Pardo JM, Batelli G, Van Oosten MJ, Bressan RA, Li X, 2013.** The Salt Overly Sensitive (SOS) pathway: established and emerging roles. *Mol Plant*, 6(2): 275-286.
- Jia T, Wang J, Chang W, Fan X, Sui X, Song F, 2019.** Proteomics analysis of *E. angustifolia* seedlings inoculated with arbuscular mycorrhizal fungi under salt stress. *Int J Mol Sci*, 20(3): 788.
- Jin T, Chang Q, Li W, Yin D, Li Z, Wang D, Liu B, Liu L, 2010.** Stress-inducible expression of GmDREB1 conferred salt tolerance in transgenic alfalfa. *Plant Cell Tissue Organ Culture*, 100(2): 219-227.
- Khan PSV, Hoffmann L, Renaut J, Hausman J, 2007.** Current initiatives in proteomics for the analysis of plant salt tolerance. *Curr Sci*, 93(6): 807-817.
- Kholghi M, Toorchi M, Bandehagh A, Ostendorp A, Ostendorp S, Hanhart P, Kehr J, 2019.** Comparative proteomic analysis of salt-responsive proteins in canola roots by 2-DE and MALDI-TOF MS. *Biochimica et Biophysica Acta (BBA)-Proteins and Proteomics*, 1867(3): 227-236.
- Kim BG, Waadt R, Cheong YH, Pandey GK, Dominguez-Solis JR, Schültke S, Lee SC, Kudla J, Luan S, 2007.** The calcium sensor CBL10 mediates salt tolerance by regulating ion homeostasis in Arabidopsis. *The Plant J*, 52(3): 473-484.
- Kopka J, Fernie A, Weckwerth W, Gibon Y, Stitt M, 2004.** Metabolite profiling in plant biology: platforms and destinations. *Genome Biol*, 5(6): 109.
- Lakra N, Kaur C, Singla-Pareek SL, Pareek A, 2019.** Mapping the 'early salinity response' triggered proteome adaptation in contrasting rice genotypes using iTRAQ approach. *Rice*, 12(1): 3.
- Lee SC, Choi DS, Hwang IS, Hwang BK, 2010.** The pepper oxidoreductase CaOXR1 interacts with the transcription factor CaRAV1 and is required for salt and osmotic stress tolerance. *Plant Mol Biol*, 73(4-5): 409-424.
- Li J, Gao Z, Zhou L, Li L, Zhang J, Liu Y, Chen H, 2019.** Comparative transcriptome analysis reveals K⁺ transporter gene contributing to salt tolerance in eggplant. *BMC Plant Biol*, 19(1): 67.
- Lim GH, Zhang X, Chung MS, Lee DJ, Woo YM, Cheong HS, Kim CS, 2010.** A putative novel transcription factor, AtSKIP, is involved in abscisic acid signalling and confers salt and osmotic tolerance in Arabidopsis. *New Phytologist*, 185(1): 103-113.
- Liu G, Li X, Jin S, Liu X, Zhu L, Nie Y, Zhang X, 2014.** Overexpression of rice NAC gene SNAC1 improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton. *PLoS One*, 9(1): e86895.
- Majoul T, Chahed K, Zamiti E, Ouelhazi L, Ghir R, 2000.** Analysis by two-dimensional electrophoresis of the effect of salt stress on the polypeptide patterns in roots of a salt-tolerant and a salt-sensitive cultivar of wheat. *Electrophoresis: An Int J*, 21(12): 2562-2565.
- Martínez C, Cosgaya P, Vázquez C, Gac S, Ganga A, 2007.** High degree of correlation between molecular polymorphism and geographic origin of wine yeast strains. *J Appl Microbiol*, 103(6): 2185-2195.
- Moons A, Bauw G, Prinsen E, Van Montagu M, Van Der Straeten D, 1995.** Molecular and physiological responses to abscisic acid and salts in roots of salt-sensitive and salt-tolerant Indica rice varieties. *Plant Physiol*, 107(1): 177-186.
- Munns R, Tester M, 2008.** Mechanisms of salinity tolerance. *Ann Rev Plant Biol*, 59: 651-681.
- Ndimba BK, Chivasa S, Simon WJ, Slabas AR, 2005.** Identification of Arabidopsis salt and osmotic stress responsive proteins using two-dimensional difference gel electrophoresis and mass spectrometry. *Proteomics*, 5(16): 4185-4196.
- Ni Y, Wang X, Li D, Wu Y, Xu W, Li X, 2008.** Novel cotton homeobox gene and its expression profiling in root development and in response to stresses and phytohormones. *Acta biochimica et biophysica Sinica*, 40(1): 78-84.
- Nuccio ML, Rhodes D, McNeil SD, Hanson AD, 1999.** Metabolic engineering of plants for osmotic stress resistance. *Curr Opin Plant Biol*, 2(2): 128-134.
- Oyiga BC, Ogbonnaya FC, Sharma RC, Baum M, Léon J, Ballvora A, 2019.** Genetic and transcriptional variations in NRAMP-2 and OPAQUE1 genes are associated with salt stress response in wheat. *Theoret Appl Genet*, 132(2): 323-346.
- Parvaiz A, Satyawati S, 2008.** Salt stress and phyto-biochemical responses of plants - a review. *Plant Soil Environ*, 54(3): 89.
- Peng C, Chang L, Yang Q, Tong Z, Wang D, Tan Y, Sun Y, Yi X, Ding G, Xiao J, 2019.** Comparative physiological and proteomic analyses of the chloroplasts in halophyte *Sesuvium portulacastrum* under differential salt conditions. *J Plant Physiol*, 232: 141-150.
- Plett DC, Møller IS, 2010.** Na⁺ transport in glycophytic plants: what we know and would like to know. *Plant Cell Environ*, 33(4): 612-626.
- Rawson H, Long M, Munns R, 1988.** Growth and development in NaCl-treated plants. I. Leaf Na⁺ and Cl⁻ concentrations do not determine gas exchange of leaf blades in barley. *Functional Plant Biol*, 15(4): 519-527.
- Roy SJ, Negrão S, Tester M, 2014.** Salt resistant crop plants. *Curr Opin Biotechnol*, 26: 115-124.

- Sadat Noori SA**, Ferdosizadeh L, Izadi-Darbandi A, Mortazavian M, Mohammad S, Saghafi S, **2011**. Effects of salinity and laser radiation on proline accumulation in seeds of spring wheat. *J Plant Physiol Breed*, 1(2): 11-20.
- Sanan-Mishra N**, Pham XH, Sopory SK, Tuteja N, **2005**. Pea DNA helicase 45 overexpression in tobacco confers high salinity tolerance without affecting yield. *Proc Natl Acad Sci*, 102(2): 509-514.
- Seki M**, Narusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, **2002**. Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. *Plant J*, 31(3): 279-292.
- Serra TS**, Figueiredo DD, Cordeiro AM, Almeida DM, Lourenço T, Abreu IA, Sebastián A, Fernandes L, Contreras-Moreira B, Oliveira MM, **2013**. OsRMC, a negative regulator of salt stress response in rice, is regulated by two AP2/ERF transcription factors. *Plant Mol Biol*, 82(4-5): 439-455.
- Shahbaz M**, Ashraf M, **2013**. Improving salinity tolerance in cereals. *Crit Rev Plant Sci*, 32(4): 237-249.
- Shang G**, Li Y, Hong Z, Liu Cl, He SZ, Liu QC, **2012**. Overexpression of SOS genes enhanced salt tolerance in sweetpotato. *J Integrat Agric*, 11(3): 378-386.
- Sheveleva E**, Chmara W, Bohnert HJ, Jensen RG, **1997**. Increased salt and drought tolerance by D-ononitol production in transgenic *Nicotiana tabacum* L. *Plant Physiol*, 115(3): 1211-1219.
- Shi X**, Wang X, Cheng F, Cao H, Liang H, Lu J, Kong Q, Bie Z, **2019**. iTRAQ-based quantitative proteomics analysis of cold stress-induced mechanisms in grafted watermelon seedlings. *J Proteom*, 192: 311-320.
- Sugihara K**, Hanagata N, Dubinsky Z, Baba S, Karube I, **2000**. Molecular characterization of cDNA encoding oxygen evolving enhancer protein 1 increased by salt treatment in the mangrove *Bruguiera gymnorrhiza*. *Plant Cell Physiol*, 41(11): 1279-1285.
- Tang M**, Liu X, Deng H, Shen S, **2011**. Over-expression of JcDREB, a putative AP2/EREBP domain-containing transcription factor gene in woody biodiesel plant *Jatropha curcas*, enhances salt and freezing tolerance in transgenic *Arabidopsis thaliana*. *Plant Sci*, 181(6): 623-631.
- Tester M**, Davenport R, **2003**. Na⁺ tolerance and Na⁺ transport in higher plants. *Ann Bot*, 91(5): 503-527.
- Thomas J**, Sepahi M, Arendall B, Bohnert H, **1995**. Enhancement of seed germination in high salinity by engineering mannitol expression in *Arabidopsis thaliana*. *Plant Cell Environ*, 18(7): 801-806.
- Tuteja N**, Sahoo RK, Huda KMK, Tula S, Tuteja R, **2015**. OsBAT1 augments salinity stress tolerance by enhancing detoxification of ROS and expression of stress-responsive genes in transgenic rice. *Plant Mol Biol Rep*, 33(5): 1192-1209.
- Ueda A**, Kanechi M, Uno Y, Inagaki N, **2003**. Photosynthetic limitations of a halophyte sea aster (*Aster tripolium* L) under water stress and NaCl stress. *J Plant Res*, 116(1): 65-70.
- Wang B**, Lutge U, Ratajczak R, **2001**. Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte *Suaeda salsa*. *J Exp Bot*, 52(365): 2355-2365.
- Wei JZ**, Tirajoh A, Effendy J, Plant AL, **2000**. Characterization of salt-induced changes in gene expression in tomato (*Lycopersicon esculentum*) roots and the role played by abscisic acid. *Plant Sci*, 159(1): 135-148.
- Xu RR**, Qi SD, Lu LT, Chen CT, Wu CA, Zheng CC, **2011**. A DEXD/H box RNA helicase is important for K⁺ deprivation responses and tolerance in *Arabidopsis thaliana*. *The FEBS J*, 278(13): 2296-2306.
- Yokoi S**, Bressan RA, Hasegawa PM, **2002**. Salt stress tolerance of plants. *JIRCAS Working Report*, 23(1): 25-33.
- Zhang H**, Deng C, Yao J, Zhang YL, Zhang YN, Deng S, Zhao N, Sa G, Zhou X, Lu C, **2019**. *Populus euphratica* JRL mediates ABA response, ionic and ROS homeostasis in arabidopsis under salt stress. *Int J Mol Sci*, 20(4): 815.
- Zhou W**, Li Y, Zhao BC, Ge RC, Shen YZ, Wang G, Huang ZJ, **2009**. Overexpression of TaSTRG gene improves salt and drought tolerance in rice. *J Plant Physiol*, 166(15): 1660-1671.
- Zhu D**, Hou L, Xiao P, Guo Y, Deyholos MK, Liu X, **2019**. VvWRKY30, a grape WRKY transcription factor, plays a positive regulatory role under salinity stress. *Plant Sci*, 280: 132-142.
- Zhu JK**, **2003**. Regulation of ion homeostasis under salt stress. *Curr Opin Plant Biol*, 6(5): 441-445.

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