Australian Journal of
Crop Science AJCS
AJCS 9(4):321-336 (2015) ISSN:1835-2707

Review Article

Molecular mechanisms of plant salinity tolerance: a review

Kaivan Bahmani*, Seyed Ahmad Sadat Noori, Ali Izadi Darbandi, Azam Akbari

Department of Agronomy and Plant Breeding Science, College of Abouraihan, University of Tehran, Tehran, Iran

***Corresponding author: kbahmani0918@ut.ac.ir**

Abstract

Accompanied with increasing world's population, we need more food. In the other hands, most important crops and vegetables are susceptible to salinity. Unfortunately the salinization process in agricultural fields will decrease the suitable land for cultivation by 30% within the next 25 years, and up to 50% by the year 2050. Therefore, developments of salt tolerant crops can be the best and most practical way to produce enough food. In the course of evolution, plants have developed several protecting mechanisms (avoidance and tolerance) so as to adapt to salt stress. Understanding the cellular basis of salt stress tolerance mechanisms is necessary for breeding and genetic engineering of salt tolerance in crops. Tolerance mechanisms mainly are applicable to practical manipulations. Tolerance mechanisms in plant can be categorized as: a)-antioxidative defense, b)-ion homeostasis, c)-compatible solute and d)-transcription factors. In this review we tried to make a comprehensive review on these 4 tolerance mechanisms from the molecular aspects.

Keywords: salinity, SOS pathway, antioxidative defense, ion homeostasis, compatible solute, transcription factor.

Abbreviations: ABA_abscisic acid, ABRE_ABA responsive element, APX_ascorbate peroxidase, CAT_catalase; CDPK_calcium dependent protein kinase, CIPK_calcineurin B like protein interacting protein kinase, DHAR_dehydro ascorbate reductase, DRE_ dehydration responsive elements, EC_electrical conductivity, GB_glycine betaine, GPX_glutathione Peroxdase; H^+PPiase_ H^+pyrophosphatase, H_2O_2_hydrogen peroxide, HKT_high affinity K transporters, LEA_late embryogenesis abundant; LCT_low affinity cation transporter, MAPK_mitogen activated protein kinase, MDHA_mono Dehydro Ascorbate; MDAR_mono dehydro ascorbate reductase , NADPH_nicotinamide adenine dinucleotide phosphate, NSCC_non selective cation channels, PRO_Proline, ROS_reactive oxygen species, SOD_superoxide dismutase, SOS_salt overly sensitive; TF_transcription factor.

Introduction

At the recent years, plant breeders have successfully done a lot of researches on molecular mechanisms of salinity tolerance led to valuable achievements, but despite of this, there are few comprehensive reviews on it. Thus, we tried to surmount this need. As the population of the earth continues to increase, more food should be produced. In the other hands, Plants as the first chain of production are ordinarily exposed to different environmental stresses, including drought, salinity, and high and low temperatures that reduce crop yield, which decrease the universal food production bfigfigffffy 70% (Batool et al., 2014; Eltelib et al., 2012; Fu et al., 2011; Shao et al., 2008; Sadat Noori et al., 2008; Vinocur and Altman, 2005; Sadat Noori and McNeilly, 2000; Pitman and Lauchli, 2002). One of the most important stresses, especially in arid regions is the Salinity (Sadat Noori et al., 2006; Nikolova and Ivancheva, 2005; Foolad, 2004; Sadat Noori and McNeilly, 2000; Shannon, 1998). Salinity could decrease the quantity and quality of plants yield (Murkute et al., 2005). The meaning of Salinity is having of electrical conductivity (ECe) 4 dS m^{-1} to up at 25˚C (Richards, 1954). The origins of salt in land can be very various but irrigation and poor drainage are the main factors important in salinization (Ezlit et al., 2010; Mohamed et al., 2007; Zhu, 2007). Cations and anions with most important role in salinity are sodium (Na^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}), chloride (Cl^-), sulfate (SO_2^{-4}) and bicarbonate (HCO^{-3}), meanwhile the most prevalent of them are firstly Na (in almost plants) and secondly Cl (especially in trees like citrus) (Ebrahimi and Bhatla, 2012; Rai et al., 2011; Brumos et al., 2009; Turkan and Demiral, 2009; Tester and Davenport, 2003; Volkmar et al., 1998). Because of that in salinity researches on plants, mostly use NaCl as the salinizing salt (Shahbaz and Ashraf, 2013; Rani et al., 2012; Izadi Darbandi and Bahmani, 2011; Sadat Noori et al., 2008; Jenks et al., 2007). Most of the eatable plants are glycophytes and susceptible to salinity, in the other hand, nearly all of the plants in reproductive stage aren't tolerant to salinity (Izadi Darbandi and Bahmani, 2011; Munns, 1993). Based on an information from FAO (The United Nations Food and Agriculture Organization), more than 400 million hectares of the world land, including most parts of the continents have the salinity problem (Koohafkan, 2012). Growing salinization phenomena in agricultural fields decreases the proper land for cultivation, even maybe up to 50% by the year 2050 (Rani et al., 2012; Tian et al., 2011; Parvaiz and Satyawati, 2008; Chinnusamy et al., 2005). In these ways, new technologies like Remote Sensing are perfectly used for identifying and mapping of saline areas (Allbed and Kumar, 2013). Elimination of Salts from the Root Zone of plants by traditional methods like irrigation correction, leaching, cultivation change, especial kind of fertilizer application, or reduction in harmful effect of salinity using some especial bacteria and mycorrhyzal fungi (like Ectomycorrhizas, Arbuscular Mycorrhizas), plant treatment (by Salicylic acid, Brassinosteroids, Abscisic acid) may be the first solutions for salinity (Plaut et al., 2013). It is reported that short term treatment of tomato plants by NaCl that was caused to increase in antioxidant content in plant (Roy and Sengupta, 2014), and also treatment of rice seeds by Prolin as one of the compatible solute (Deivanai et al., 2011) can increase salt tolerance of these plants.

Unfortunately, sometime these solutions are not working. As the last solution, Development of salt tolerant crops by classical or modern techniques of plant breeding would be an applied approach for salinity (Izadi Darbandi and Bahmani, 2011; Sadat Noori et al., 2006; Yamaguchi and Blumwald, 2005; Chinnusamy et al., 2005; Sadat Noori and McNeilly, 2000).

Plants in saline condition

Plants can sense salt stress by ionic (Na) and osmotic signals. Excess Na is sensed either by the transmembrane protein on the plasma membrane (Membrane bound histidine kinases) or within the cell by Na sensitive enzymes or membrane proteins. Also the plasma membrane Na^+/H^+ antiporter SOS1with 10-12 transmembrane domains and a long cytoplasmic tail can work as a Na sensor (Ji et al., 2013; Turkan and Demiral, 2009; Chinnusamy et al., 2005; Mikami et al., 2002). Salinity has several deleterious effects on plants such as: Osmotic stress (resulted in loss of cell turgor), Ion toxicity (mainly due to the Na^+ and Cl^- and SO_4^{2-}), Mineral deficiency (specially Potassium, Ferrum and Zinc), Ion imbalance, Oxidative stress, Stomatal blockade (resulted in reduction of carbon dioxide availability), photosynthesis Prohibition, cell division Prohibition (interaction of Salinity with plants cellular components including DNA, proteins, lipids and pigments), increase of sensitivity to diseases and a combination of these (Fahramand et al., 2014; Rani et al., 2012; Aslam et al., 2011; Tester and Davenport, 2003; Zhu, 2002; Volkmar et al., 1998; MacDonald, 1982; Snapp et al., 1991). Also decrease in PSII Photochemistry and Chlorophyll Content because of salinity and subsequently reduction in photosynthesis and yield production in plants is confirmed (Afzal et al., 2014; Jamil et al., 2014; Ashraf and Harris, 2013). Genotype, environment and genotype by environment (G_xE) interactions are major factors that evolutionary influence features of plants, so due to adaptation to the local environments, different genotypes show genetic variation which may impact on the traits of plants including salinity resistance (Bahmani et al., 2012a; Izadi Darbandi and Bahmani, 2011; Heywood, 2002). As a sidelong point, this shows the importance of genetics conservation (Bahmani et al., 2012a; Bahmani et al., 2012b; Bahmani et al., 2013).

Plant adaption to salinity (avoidance and tolerance)

Plants with the power of living in saline environments may have avoidance (plant morphological, anatomical and physiological changes) or/and tolerance (cellular and molecular approaches) mechanisms (Fu et al., 2011; Ashrafijou et al., 2010; Vinocur and Altman, 2005). Salt resistance plants known as Halophytes, have an important mechanism of avoidance (plant tries to keep away the salt ions) and better at regulation Na transport than glygophytes. The avoidance mechanisms mostly result of morphological and physiological changes at the whole-plant level (Kumar Parida and Jha, 2010; Tester and Davenport, 2003). Some tactics of salt avoidance in halophytes including:

1. Exclusion: passive and active rejection of ions (The most common way of sustaining in high salinity occurring at the roots)
2. Secretion (salt gland and hair on aerial parts of plants responsible for the concealment of excess salt)
3. Shedding (in some plants, removing of old leaves that excess salts have accumulated in them)
4. Succulence (thick leaves of succulent plants have larger mesophyll cells, smaller intercellular spaces, decreased surface area and higher water content)
5. Stomatal response (either guard cell uses K in place of sodium to obtain it's normal turgor or may uses K to limit Na intake, this mechanism is important in those halophytes that lack glands) (Roy et al., 2014; Batool et al., 2014; Aslam et al., 2011; Kumar Parida and Jha, 2010; Vinocur and Altman, 2005; Volkmar et al., 1998; Flowers et al., 1986)

Avoidance mechanisms chiefly are not very accountable to practical manipulations. Tolerance mechanism is plants ability to grow and develop on the saline condition through cellular and molecular biochemical modifications that is amenable to practical manipulations. Most of avoidance mechanisms are reliant upon some other mechanism at the cellular level (Vinocur and Altman, 2005). In recent decades, there are a numerous articles about successful development of salinity tolerance in plants by classical breeding, including Landrace assessment and screening (Roy and Sengupta, 2014; Sadat Noori, 2005; Sadat Noori and McNeilly, 1999), Transgressive Segregation (Shahbaz and Ashraf, 2013; Sadat Noori and Harati, 2005), Triple Test Cross (Sadat Noori and Sokhansanj, 2004) and even artificial neural network (Sadat Noori et al., 2011a), although these methods are full of difficulties. As the first step for screening program for salinity tolerance or any kind of desirable traits it is important to investigate the heritability of the good traits (Izadi Darbandi et al., 2013). Plant breeders need to deploy the new techniques such as Laser and biotechnological tools. Up to now there are several reports about improving salt tolerance in the plant by Laser (Sadat Noori et al., 2011b; Ashrafijou et al., 2010), but because of lack of enough information on its heritability and consequent effects, biotechnological tools for search in crucial problems of crop improvement for sustainable agriculture are more popular. Genetic engineering for developing tolerant plants provides a faster way to improving the crops (Hossain et al., 2007). Genetic engineering as a solution to abiotic stress tolerance is based on introgression and expression of genes involving in signaling and controlling pathways or genes encoding proteins producing stress tolerance or enzymes related to pathways resulting in the functional and structural metabolite synthesis (Roy et al., 2014; Vinocur and Altman, 2005). In the way of introduction of Salinity tolerance by genetic engineering, candidate genes are encoding; (1) antioxidants and detoxifying enzymes, (2) ion transport, (3) compatible solutes, (4) transcription factors and (5) late embryogenesis abundant proteins (Roy and Sengupta, 2014; Roy et al., 2014; Shang et al., 2012; Jenks et al., 2007). Because salinity mechanisms doesn't have 100% efficiency, hence plant breeders to improve salinity tolerance of plants should deal with that by using several mechanisms instead of using just one (Batool et al., 2014; Yamaguchi and Blumwald, 2005; Chinnusamy et al., 2005; Murkute et al., 2005).

Molecular mechanisms of salinity tolerance

There are myriad of Kinases, phosphatases and transcription factors in plant that are related to salinity responses and/or tolerance including: Heat shock factor (HSF), C-repeat-binding factor/dehydration-responsive element binding protein (CBF/DREB), ABA-responsive element binding factor/ABA-responsive element (ABF/ABRE) families), Osmosensors (like AtHK1), Phospholipid-cleaving enzymes (like PLD), Second messengers (like Ca^{2+}, PtdOH, ROS), Metabolic phosphatases (like HAL2), Ca-dependent protein kinases (CDPKs), Serine/threonine protein kinase (like SOS2), Mitogen-activated protein kinase (like MAPK) cascades, Two component histidine kinases, Ca/calmodulin-activated serin/threonine-specefic protein phosphatases (Vinocur and Altman, 2005; Halfter et al., 2000; Kovtun et al., 2000; Gilmascarell et al., 1999; Urao et al., 1999; Kudla et al., 1999; Pardo et al., 1998). Although in plant resistance to biotic stresses rather than simply controlled, but Salinity tolerance as one of the abiotic resistance is controlled by the interaction of several genes (few major genes along with several minor genes) (Batool et al., 2014; Ashraf, 2009; Mahajan et al., 2008; Sadat Noori et al., 2006; Ashraf and Harris, 2004). Since salinity tolerance is polygenic, so it includes a myriad of physiological and biochemical processes interacting with one another to resist to salt at molecular, cellular or whole plant levels (Ismail et al., 2014; Shahbaz and Ashraf, 2013; Vinocur and Altman, 2005; Mishra et al., 1998; Volkmar et al., 1998). Salt tolerance mechanism is even getting more intricate in when a tolerance varies at different stages of plant life (Shahbaz and Ashraf, 2013; Izadi Darbandi and Bahmani, 2011; Sadat Noori et al., 2008; Sadat Noori and Sokhansanj, 2008; Sadat Noori and McNeilly, 2000). Activation of molecular networks cascades related to stress perception, transduction of signal (started from the roots and resulted in cellular and whole plant levels) and the specific gene expression and metabolites, are determining factors of Plant adaptation to environmental stresses (Ismail et al., 2014; Ashraf, 2009; Vinocur and Altman, 2005). To sustain against the harmful effects of salinity stress, plants have evolved several biochemical, morphological and molecular mechanisms with their signal transduction. Other important things about salt tolerance are the ability of plant in: 1- Right time of signal transduction (as it is reported activation of stress signals are temporarily) and 2- Organization of the several arose stress signal transduction that mostly are mixed with each other (Ismail et al., 2014). So salinity tolerance is not a simple mechanism. In crops for succeed in breeding and genetic engineering to salinity tolerance introduction, complete understanding of the molecular basis of tolerance mechanisms is necessary. The most important salinity tolerance mechanism including antioxidative defense system, ion homeostasis, accumulation of compatible solutes and transcription factors (Roy and Sengupta, 2014; Roy et al., 2014; Shang et al., 2012; Jenks et al., 2007) have been explained below.

I. Antioxidative defense system

The reactive oxygen species (ROS) including superoxide (O^{2-}), hydrogen peroxide (H_2O_2), hydroxyl radical (•OH), and singlet oxygen ($1O_2$) are free radicals that are atoms or groups of atoms with at least one unpaired electron tending to pair up to give rise stable two electron bonds. ROS are very reactive and interact with cellular molecules and metabolites resulting in several destructive processes and cellular damage (Eltelib et al., 2012; Ashraf, 2009; Turkan and Demiral, 2009; Mahajan et al., 2008). Anyway, ROS also play an important role in some important physiological process, for example cell signaling, gene regulation, senescence, programmed cell death and pathogen defense (Eltelib et al., 2012; Ashraf, 2009; Mahajan et al., 2008; Foyer and Noctor, 2005; Apel and Hirt, 2004; Ashraf and Harris, 2004; Zhu, 2002; Mittler, 2002; Polle, 2001; Hernandez et al., 2001). ROS can be produced even during normal aerobic metabolism in mitochondria and chloroplasts from the electron transport chains electrons are escaped and react with O_2 while there are no any other acceptors. At the time of salinity stress and consequently osmotic stress, CO_2 availability for photosynthetic carbon assimilation because of stomatal closure, is limited. This even leads to over reduction of electron in the photosynthetic transport chain, so causing the production of ROS, in that respect causing high accumulation of superoxide in chloroplast and finally photoinhibition and photooxidation damage. Other stresses, although like pathogens, salinity, water logging, temperature extremes, high light intensity, herbicide treatment or mineral nutrient deficiency can lead to ROS production. In a normal development situation for a plant, the ROS production is as low as $240 \mu MS^{-1}$ superoxide in cell and $0.5 \mu M$ H_2O_2 in the chloroplast, while in salinity situation, the level of ROS production would be up to $720 \mu MS^{-1}$ and H_2O_2 level up to $15 \mu M$. During the evolution, plant has created an antioxidant defense system enzymatic (SOD, APX, GPX, GR, CAT and…) and non-enzymatic (ascorbic acid, glutathione, some osmolytes, SOS1 in SOS pathway, carotenoids, flavonoids, glutathione, flavones, tocopherols, anthocyanins, and...) (Eltelib et al., 2012; Aslam et al., 2011; Ashraf, 2009; Hossain et al., 2007; Katiyar et al., 2006; Chen and Murata, 2000; Noctor and Foyer, 1998; Bohnert and Jensen, 1996; Liu and Zhu, 1992). Plants can get rid of superoxide with superoxide dismutase (SOD) help, which catalyzes the superoxide into hydrogen peroxide (H_2O_2) and oxygen, and also SOD is important in hindering the reduction of metal ions and hydroxyl radical synthesis (Turkan and Demiral, 2009; Parida and Das, 2005). On the other hand, Absesic Acid (ABA) is able to induce enhanced production of H_2O_2, which also act as a second messenger to adjust antioxidant defense genes in abiotic stresses (Roy and Sengupta, 2014; Guan et al., 2000; Pei et al., 2000). This H_2O_2 damaging to proteins and DNA and causing lipid peroxidation, is eliminated by peroxidase and catalase (Hossain et al., 2007). Catalase (CAT) is catalyzing the reduction of H_2O_2 to water in chloroplasts. Peroxidases are divided into two types:

a) The Ascorbate peroxidase (APX) one of the most important peroxidase located in the chloroplast, cytosol, mitochondria, apoplast and peroxisomes: Ascorbate by APX is catalyzing the reduction of H_2O_2 to water (Turkan and Demiral, 2009; Noctor and Foyer, 1998). Then this ascorbate would transform to MDHA (Mono Dehydro Ascorbate), the produced MDHA can retransform into the Ascorbate through:

a-1- MDHA would transform to Ascorbate by Mono Dehydro Ascorbate Reductase (MDAR) by the help of NADPH (Nicotinamide Adenine Dinucleotide Phosphate)

a-2- When Dehydro ascorbate reductase (DHAR) reduced glutathione (GSH) to transform to GSSG, also MDHA by DHAR would transform to Ascorbate. Glutathione reductase (GR) is maintaining the GSH (reduced glutathione)/GSSG (oxidized glutathione) ratio favorable to dehydro ascorbate reduction.

b) The Glutathione Peroxdase (GPX) in peroxisomes: GSH through APX is catalyzing the reduction of H_2O_2 to water (Eltelib et al., 2012; Rai et al., 2011; Ashraf, 2009; Turkan and Demiral, 2009; Foyer and Noctor, 2005) (figure 1).

Recently an article was published reporting when reactive oxygen species like H_2O_2 is damaging metabolic processes, external application of ascorbic acid can decrease these damages through synergistic functions with other antioxidants, and membranes stabilizing (Mohsen et al., 2014). Sensors of ROS could include redox sensitive receptors-like kinases and two component histidine kinases activating a mitogen activated protein kinase (MAPK includes ATMPK3, ATMPK4 and ATMPK6) module. Salinity stress initiates activation and intensify the gene expression of a MAPK signaling cascade, some components of them are shared for both salt and ROS (Chinnusamy and Zhu, 2003). In Arabidopsis Salinity stress with ROS signaling could transduce via ANP1 (a MAPKKK), AtMPK3, and AtMPK6 along with its positive regulator Nucleoside Diphosphate Kinase 2 (AtNDPK2) (Ashraf and Harris, 2013; Kovtun et al., 2000; Moon et al., 2003). Promoters of genes encoding ROS detoxifying enzymes include antioxidant responsive elements (ARE), ABA responsive elements (ABRE), heat shock elements (HSE), and redox-regulated transcription factors: nuclear factor kappa-B (NFkB) and the activator protein-1 (AP-1) recognition cis-elements (Vranova et al., 2002). In levels of expression and activity of antioxidative enzymes their differences that sometimes connected to more tolerant plant (Roy and Sengupta, 2014; Munns and Tester, 2008; Mittova et al., 2002). The expression of the tobacco mitogen-activated protein kinase kinase kinase/ Nicotinia protein kinase 1 (MAPKKK/NPK1) in maize activates an oxidative signal cascade and resulted in salinity tolerance in the transgenic plants (Vinocur and Altman, 2005).

Transgenic overexpression of NPK1 in tobacco (Kovtun et al., 2000), NDPK2 in Arabidopsis (Moon et al., 2003), OsMAPK5 in rice (Xiong and Yang, 2003), increased tolerance to several abiotic stresses including salt stress by enhancing ROS detoxification is possible. Some genes from different origin have identified that are helping to cause antioxidative defense and utilized in many plants as cause of tolerance, including: *Mn-SOD*, *DHARI*, *Gly I* and *Gly II*, *Chl-APX5*, *TPX2*, *KatE*, *GST*, *GPX* and … (Ashraf, 2009).

II. Ion-homeostasis

Salinity interrupts homeostasis ion distribution and water potential at cellular and whole plant levels (Tunuturk et al., 2011; Zhu, 2001). When K substitute by Na in biochemical reactions then Ion cytotoxicity is happening and when Na and Cl ions interfere with noncovalent interactions between their amino acid, then proteins don't function, thus in salinity condition poisonous levels of sodium and also inadequate amount of K for enzymatic reactions and osmotic adjustment is happened (Munns et al., 2006; Ashraf and McNeilly, 2004; Zhu, 2002). Potassium is necessary in high concentrations, and functions in the cell through direct interacting in enzyme activation, stabilization of protein synthesis, and neutralization of negative charges on proteins (Pandolfi et al., 2012; Marschner, 1995; Perrenoud, 1990) also the positive correlation between potassium content and final yield in different crops was reported (Rameeh, 2013; Bandeh Hagh et al., 2008; Ashraf and McNeilly, 2004). When potassium shortage is happened, acidification and sodium transport are increased (Batlle and Kurtzman, 1985; Kurtzman, 1990).

Despite of potassium, sodium is necessary in very low concentrations for some plant species and is deadly in high concentrations (Marschner, 1995). Chlorine (Cl) is necessary micronutrient for higher plants. Chloride as an active solute in vacuole is included in the adjustment of turgor and osmosis.

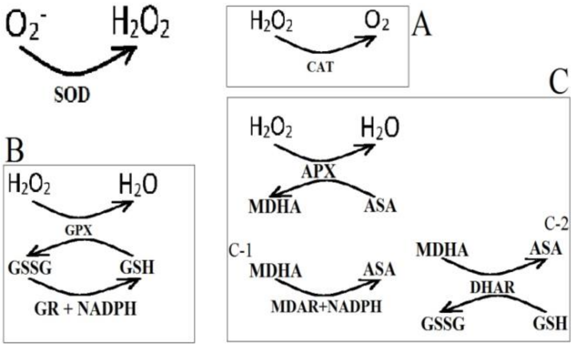

Fig 1. Antioxidative defense system. A: Catalase (CAT) is catalyzing the reduction of H_2O_2 to water. B: GSH through APX is catalyzing the reduction of H_2O_2 to water. C: Ascorbate by APX is catalyzing the reduction of H_2O_2 to water then this ascorbate would transform to MDHA (Mono Dehydro Ascorbate), the produced MDHA can retransform into the Ascorbate through C-1: Mono Dehydro Ascorbate Reductase (MDAR) by the help of NADPH (Nicotinamide Adenine Dinucleotide Phosphate), C-2: When Dehydro ascorbate reductase (DHAR) reduced glutathione (GSH) to transform to GSSG.

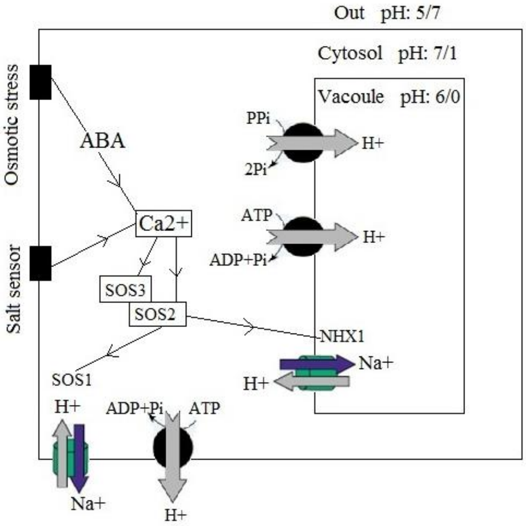

Fig 2. Ion homeostasis mechanism. In this figure, SOS pathway, H^+ATPase and H^+PPiase and Absesic acid signaling pathway were shown.

Chloride in the cytoplasm can control the activities of key enzymes. Furthermore, Cl flow is included in the stabilization of membrane potential, regulation of intracellular pH gradients and electrical excitability (White and Broadley, 2001). Always cytoplasmic concentration of potassium is relatively high; meanwhile concentration of Na is relatively low, indicating K selective uptake and maybe Na preferential rejection. In animal cells, the low cytoplasmic Na concentration is kept by Na:K ATPases, and the inward gradient for Na is in favor of uptake of many solutes. Low Na concentrations in plant cells are kept by the proton gradient generated by proton pumps located in the plasma membrane

(Schachtman and Liu, 1999). Dicotyledon plants, because of their ability to accumulate most of the Na in their vacuole and also comparatively little need to K for cytosolic metabolism, have higher shoot Na and Na/K ratio, versus monocotyledon plants have less Na storage capacity and need more K and compatible osmotic for their cytosolic metabolism (Flower and Yeo, 1988; Glenn et al., 1999). In plants, there are some highly K-selective channels, but there is no highly Na-selective channels (Hille, 1992). Potassium can be uptake through 1-Potassium-selective uptake channels (like AKT), 2-K high-affinity transporters (HKT and HAK), 3-Non-selective cation channels (NSCC that are permeable to monovalent cations) in root cells (current in one direction into the cytoplasm) and 4-Low-affinity cation transporter (LCT1) (Roy et al., 2014; Essah et al., 2003; Hirsch et al., 1998).

Initial motion of Na from the soil solution into the root cortical cytoplasm is passive (Cheeseman, 1982). Na ion can entry into the cell through three pathways listed below:

a) HKT: external side of the cells for uptake Na competes with K. As we know K and Na ions in ionic radius and ion hydration energies are similar (Hille, 1992), and in salinity condition high affinity K transporters (HKT) act as usually high affinity Na transporters (Plett and Moller, 2010: Pilot et al., 2003; Zhu, 2003; Schachtman and Liu, 1999). It was reported Antisense expression of wheat *HKT1* in transgenic wheat causes significantly less Na uptake and enhances growth under salinity (Laurie et al., 2002).
b) Apoplast pathway: Another way for Na entry is leakage into the root through apoplast. Sodium entry into root cell cytosol through cation channels (AKT1, NORC and NSCC) either selective or nonselective. Na can entry into the root xylem stream via an apoplastic pathway (Plett and Moller, 2010; Yamaguchi and Blumwald, 2005; Chinnusamy et al., 2005; Rus et al., 2001; Maser et al., 2002). Halophytes have several anatomical adaptations to reduce salt apoplastic entry. The width of casparian band is broader in halophytes than in non-halophytes and the interior layer of cortical cells can differentiate into a second endodermis (Tester and Davenport, 2003). It is reported in cotton implementation of salinity treat to seedlings accelerate the casparian strip formation and induce exodermis formation (Tester and Davenport, 2003).
c) LCT1: There is a non-selective and low affinity cation transporter (LCT1) to uptake monovalent cations like Rubidium, Potassium, Sodium and divalent cations like Calcium and Cadmium ions, allow Na to entry into the cell (Plett and Moller, 2010; Schachtman and Liu, 1999).

Chloride, through symplastic pathway, Cl fluxes across the plasma membrane and tonoplast of root cells, gets into plants adjusted by root Cl content. In plant Chloride is moveable. The transmembrane voltages and Cl activity assessments in cells imply that:

a) In saline situation Cl enters into the plants by passive Cl influx while in not very saline situation active Cl transport through the plasma membrane (Cl channel family and Cation Cl Cotransporter (CCC) family) is in work.
b) Active and passive transports of Cl happen at the tonoplast. Influx or efflux of Cl from side to side of the plasma membrane is mediated by electrogenic Cl/2H symporter in plasma membrane of root-hair cells and Cl channels. In a similar manner, fluxes of Cl in every direction across the tonoplast are provided by Cl channels and influx of Cl to the vacuole is provided by Cl/nH antiport (Ebrahimi and Bhatla, 2012; Brumos et al., 2009; White and Broadley, 2001).

One of the other ion that may have detrimental effects on plant is Lithium, so that, it is necessary to introduce the family of sodium/proton (Na^+/H^+) antiporters. In Arabidopsis, about 44 genes encoding H-attached transporters have recognized (Rani et al., 2012). These transporters are divided into three groups:

a. CPA1 (NHX, eight members)
b. NhaD (two members)
c. CPA2 (including CHX, twenty eight members; KEA, six members)

The eight members of CPA1 family (AtNHX1-8), six are vacuolar/endosomal Na^+/H^+ antiporters AtNHX1-6, and two are plasma membrane Na^+/H^+ antiporters (AtNHX7-8 (AtNHX7 is SOS1)).

NHX homologues have recognized in diverse plants and the importance of them has emphasized with salt tolerant transgenic plant production overexpressing NHX genes (Roy et al., 2014; Apse and Blumwald, 2007). AtNHX1, AtNHX2, AtNHX5, AtNHX6 and AtNHX7/SOS1 have described as functional Na^+/H^+ antiporters. Low potassium tolerance in Arabidopsis is provided by AtNHX3 encoding a K^+/H^+ antiporter. An important agent in Arabidopsis responses to salt stress is AtNHX4 that would be expressed after sensing of salt stress or/and abscisic acid. AtNHX4 transports Na^+ from vacuolar to cytosol, so AtNHX4 expression makes cell sensitive to salinity. AtNHX8 is described as a plasma membrane Li^+/H^+ antiporter (Brett et al., 2005; Rani et al., 2012). Lithium (Li^+) with its specific carriers is another influential toxic ion for plant metabolism. AtNHX8 encodes plasma membrane Li^+/H^+ antiporter that work in the way of Li^+ detoxification and keeping of ion homeostasis in Arabidopsis (An et al., 2007). Anyway, after these Na is the most detrimental ion. A high K/Na ratio in the cytosol is needed for normal cell functions, so that it is very more important than simply keeping low Na concentration (Yue et al., 2012; Pandolfi et al., 2012; Amtmann and sanders, 1999; Gorham et al., 1990). In saline situation, after entering Na into the cell, the level of toxicity of Na is greatly a result of its ability to compete with K to bind to essential sites for cellular function. It is worth to say, More than 50 enzymes are activated by K, and Na cannot do that (exception of high ability of Na to binding rather than K), so various enzymatic processes can disrupt. In addition, protein synthesis demands high K concentration, K is necessary for the binding of tRNA to ribosome function, so at the present of Na the protein synthesis disruption would be happening (Tester and Davenport, 2003). From the aspect of the salinity tolerance, the existing genetic diversity in plants is usually connected to keep a high concentration of necessary ions like K^+ and keep the concentration of toxic ions like Na^+ below a threshold level of toxic ions in cytosol. Plants can do this by adjusting the expression and activation of K^+ and Na^+ transporters and of H^+ pumps generating the driving force to transport. In addition to these mechanisms, Na secretion is a strategy used by some halophytic plants (Rai et al., 2011; Mahajan et al., 2008; Zhu, 2003; Yamaguchi and Blumwald, 2005; Amtmann and Sanders, 1999). In woody perennial plants, such as citrus and grape, genetic diversity for salt tolerance is connected to capacity to exclude Cl ions and keep Na in woody stem and roots (Murkute et al., 2005; Tester and Davenport, 2003; Munns, 1993; Storey and Walker, 1999).

II.I. SOS pathway

Detrimental effects of Na are connected with the Na accumulation in leaf tissues leaded to older leaf necrosis, beginning from top and borders and coming back to throughout of the leaf. Necessary time to appear Na damages is related to the rate of Na accumulation in leaves, and on the effectiveness of Na compartmentation in cells and leaf tissues (Ji et al., 2013; Munns, 2002; Tester and Davenport, 2003). So let's be more specific about Na. Existing of stress outside of the cells is firstly sensed the membrane receptors that signaling cascade within a cell and generation of secondary signal molecules. Reduction in calcium content because of salinity in intercellular space is less than a reduction in the cell cytoplasm. Sodium restrains the radial movement of calcium in symplastic pathway more than in the apoplastic pathway. The cell wall has a significant role in supplying calcium for the apoplastic pathway. Calcium reallocation from cell wall to intercellular space is due to its tendency towards xylem through the apoplastic pathway. This is a tactic to increase calcium loading to xylem and to decrease calcium shortage in young leaves in saline condition (Ebrahimi and Bhatla, 2012). Salinity stress commences calcium signaling network. The Ca^{2+} release can be firstly from sources out of cells (apoplastic space) by EGTA or BAPTA blocked calcineurin-mediated activity (a calcium-binding protein phosphatase- 2B protein in yeast and animal cells). BAPTA (1, 2 - Bis (o-Amino Phenoxy) ethane-N,N,N',N'-Tetraacetic Acid) is a calcium-specific aminopolycarboxylic acid and EGTA (ethylene glycol tetraacetic acid) is an aminopolycarboxylic acid. EGTA and BAPTA both is a kind of chelating agent. Also Ca^{2+} release may results from activation of PLC (phospholipase C), leading to PIP2 hydrolysis (Phosphat Idylinositol 4, 5-bis Phosphate or PtdIns(4,5)P2, also known simply as PIP2) to IP3 and subsequently Ca^{2+} release from intracellular Ca^{2+} supplies (Mahajan et al., 2008). Non-Selective Cation Channels (NSCC) that entries Na^+, are sensitive to calcium and entries Ca into the cell, and this means the inhibition of Na^+ entry into roots by calcium, so the Ca concentration in cytosol would be temporarily increased (Turkan and Demiral, 2009; Zhu, 2003 and 2001; Kopittke and Menzies, 2004; Sanders et al., 1999). Calcium controls ion transport and selectivity (Tuteja and Mahajan, 2007; Mahajan and Tuteja, 2005; Cramer, 2002). Calcium sensor, calcineurin B-like proteins (CBLs), and their interacting partners CBL-interacting protein kinases (CIPKs) play a significant role in plants in response to increased calcium and stress signaling. CIPK initiates a phosphorylation cascade, that serially regulate down-stream process (Tuteja and Mahajan, 2007; Luan et al., 2002; Batistic and Kudla, 2004; Mahajan et al., 2006). As a consequence of salt stress and an increase in intracellular Ca^{2+} levels through the mentioned mechanisms, this increase in Ca^{2+} is perceived by calcium-binding protein SOS3 in SOS pathway (Shang et al., 2012). One of the most significant main reactions to salinity is controlling pathway of Salt Overly Sensitive (SOS) that are hypersensitive to NaCl and functions in the way of Na^+ transport. The most significant part of SOS pathway is SOS1 gene encoding Na^+/H^+ transporter in the plasma membrane. In addition to its role as a Na transporter, SOS1 has a large cytosolic domain including Na sensor. The expression of SOS1 is ubiquitous, but very effective in epidermal cells surrounding the root-tip and parenchyma cells bordering the xylem (Plett and Moller, 2010; Tester and Davenport, 2003; Shi et al., 2002). The SOS1 gene was firstly identified as a genetic locus necessary for salt tolerance in Arabidopsis (Wu et al., 1996) and more studies describe its details (Shi et al., 2000). The SOS1 transcript level is highly up regulated in reaction to NaCl stress through SOS3 / SOS2 pathway, but is not up regulated by ABA (abscisic acid) or cold stress. It is worth to say that, SOS1 mRNA was more plentiful in roots than in shoots. The up regulation of SOS1 is facilitated by SOS3/SOS2 pathway (Ji et al., 2013; Mahajan et al., 2008). SOS2 also interacts with ABI2. ABI2 may dephosphorylate the proteins that are phosphorylated by SOS2 to return back to previous homeostasis after saline condition (Mahajan et al., 2008). After binding with Ca^{2+}, SOS3 alters its structure in calcium relying way, and physically interacts with serine/threonine protein kinase SOS2. The *SOS3-SOS2* complex phosphorylates and activates SOS1 to stimulate the Na^+/H^+ antiporter (NHX-type transporters from CPA1) activity in the plasma membrane (Ji et al., 2013; Tian et al., 2011; Mahajan et al., 2008; Qui et al., 2002; Guo et al., 2004). Also SOS2 activates the Na^+/H^+ antiporter activity on the vacuolar membrane directly and indirectly (Tian et al., 2011; Zhu, 2003). In normal situation, NHX-type transporters mediate H-coupled K^+ transport, cooperate in ion homeostasis and cell expansion (Venema et al., 2003). SOS1 also has a role in detoxification of ROS since it interacts with RCD1 (an important transcriptional controller of oxidative stress responsive genes) under saline and oxidative stress (Katiyar et al., 2006). Extracellular Mg^{2+} as a similar element to Ca^{2+}, has a negative effect on the Na influx that strengthen the hypothesis of Ca^{2+} on salinity tolerance (Tester and Davenport, 2003; Davenport and Tester, 2000; Schachtman and Liu, 1999; Volkmar et al., 1998), As a fine point you may know why some farmers are adding calcareous materials to their saline land (Mohamed et al., 2007). Recently, SOS4 and SOS5 have also been characterized. SOS4 is encoding a pyridoxal (PL) kinase involving in the biosynthesis of pyridoxal-5-phosphate (PLP) and an active form of vitamin B6. SOS1 contains a putative pyridoxal-5-phosphate binding motif in the C-terminal cytoplasmic tail (Zhu, 2002) so SOS4 may has a positive effect on SOS1. SOS5 has shown to be a presumed cell surface adhesion protein required to maintain normal cell expansion. Under salt stress, the normal growth and expansion of a plant cell becomes even more important, and SOS5 helps in keeping of cell wall wholeness and formation (Mahajan et al., 2008).

It is mentioned that Na^+/H^+ antiporters in plasma and vacuolar membrane are activated by the SOS pathway and process of Na compartmentation would be occurred. Also, it should be mentioned that Na leaking back out of the vacuole is another occurrence. In parallel with the Na pumping into vacuole, Na may leaks back into the cytoplasm through ion channels. These Non Selective Cation Channels such as SV and FV channels are especially plentiful in the vacuole membrane of plant cells that are highly permeable to Na as well as other cations. Depending on the ability of cells to Na sequester and also Na leaking back, the last process could readily cause problems for plant cells. Anyway the activity of mentioned channels in term of permeability to cytotoxic cation is low (Demidehik et al., 2002 and 2002). After the first recognition of the tonoplast Na^+/H^+ antiporter in barley root tips (Ratner and Jacoby, 1976), many Na^+/H^+ antiporter genes have been identified in plants, such as Arabidopsis thaliana, Oryza sativa, Atriplex gmelini, Beta vulgaris, Gossypium hirsutum and... . In spite of SOS1, the tonoplast Na^+/H^+ antiporter *NHX1* gene is induced by both salinity and the ABA. The *AtNHX1* promoter contains putative ABA responsive elements (ABRE) (Shi and Zhu, 2002). The overexpression of Na^+/H^+ antiporter genes could increase tolerance under saline conditions in transgenic Arabidopsis, tomato, Brassica, rice and wheat. These works demonstrated that Na^+/H^+ antiporter genes were crucial to plant salt-tolerance, and they could be used in crop improvement by genetic transformation technique (Pandolfi et al., 2012; Dorani Uliaie et al., 2012; Tian et al., 2011). Na^+ compartmentation into the vacuole is a frugal way of inhibiting Na^+ toxicity in the cytosol, furthermore, that Na^+ could be used as an osmolyte in the vacuole to help to gain osmotic homeostasis. Many of the salt tolerant plants (halophytes) lean on this tactic (Pandolfi et al., 2012; Yamaguchi and Blumwald, 2005; Flowers et al., 1977). This tactic has been emphasized by some experiments in which over expressing of the vacuolar antiporter (*NHX1*) and SOS genes have increased the salinity tolerance (Shang et al., 2012; Leidi et al., 2010) and there are some reports supporting this; Arabidopsis (Shi et al., 2003; Apse et al., 1999), Tomato (Zhang and Blumwald, 2001), *Brassica napus* (Zhang et al., 2001) and rice (Fukuda et al., 2004). It should be mentioned that SOS2 has some other functions like: 1. The Ca^{2+} content in the cytoplasm is naturally very low and is controlled by membrane-bound transporters. Intracellular level of calcium must be kept as low as 0.1–0.6 μM within the cytosol to preventing phosphate precipitation. SOS2 activates the Ca^{2+}/H^+ antiporters (*CAX1*) in vacuolar membrane transporting Calcium into the vacuole (for preventing of over accumulation of Calcium and also use in osmotic homeostasis), 2. Activates H^+ATPase and H^+PPiase in the vacuolar membrane (generation of driving force for transport) and 3. In Arabidopsis, AtCBL10, a calcium sensor, directly interact with SOS2 complex and work in salt extrusion at the plasma membrane level and also its sequestration into vacuole at tonoplast level (Ebrahimi and Bhatla, 2012; Kim et al., 2007; Quan et al., 2007; Cheng et al., 2004; Zhu, 2003).

II.II. H^+ATPase and H^+PPiase

Because of the acidification caused by V-type H-ATPase and H-PPase (generation of driving force for Na transport by Na^+/H^+ antiporters), Na sequestration into the vacuole also leans on expression and activity of these two pumps (Chinnusamy et al., 2005; Gluck and Al-Awqati, 1984; Doucet and Marcy, 1987; Garg and Narang, 1988). H^+ transporting by H^+ATPase in the plasma membrane and vacuolar membrane, and H^+PPiase (or pyrophosphatase protein) in the vacuolar membrane generates gradients of pH and electrical potential difference between cell and vacuole membranes. Plasma membrane Na^+/H^+ antiporter would provide with a necessary power to exclusion Na^+ out of the cell or into the vacuole and subsequent reduction of Na^+ in cytosol by intensification in proton pumping activity (Rai et al., 2011; Plett and Moller, 2010; Turkan and Demiral, 2009; Batelli et al., 2007).

Overexpression of AVP1 gene, a vacuolar H-pyrophosphatase in Arabidopsis increases Na sequestration into the vacuole and keeps higher relative water content in leaves and led to salinity tolerance (Gaxiola et al., 2001). By keeping in mind that vacuole is a store it is important for cell to have a large vacuole for Na sequestration (Shi et al., 2002). There is an electroneutral H^+K^+/ATPase in plasma membrane keeping the K^+ content in cytosol. Potassium emptying in cytosol increases the activity of the H^+K^+/ATPase to keep potassium homeostasis, and does not have any effect on H^+ATPase activity (Turkan and Demiral, 2009; Ashraf and Harris, 2004; Eiam Ong et al., 1993; Khadouri et al., 1991; Garg and Narang, 1990).

As the most important proton pump, let's talk a little more about H^+ATPase enzyme. The major role of plasma membrane H^+ATPase by mean of proton is activation of symport or antiport. For example, mineral absorption from soil to plant and also the transport of organic compounds can happen against concentration gradients with the power supplied by the electrochemical gradient generated across the plasma membrane. It should be said that many sugar/proton and amino-acid/proton symports have been identified (Plett and Moller, 2010; Chinnusamy et al., 2005; Morsomme and Boutry, 2000).

H^+ATPase has some other important functions in plant, including: 1-The opening and closing of stomata (provide the electrochemical potential necessary for ion movement), 2-Maintaining of the internal pH at 7.5 (Acidification of the cytosol activate the H^+ATPase and increase the proton extrusion) and 3- begins cellular expansion (Acidification of the external medium by plasma membrane H^+ATPase begins cellular expansion with the mechanism of "acid growth theory" that is referred to auxin) (Morsomme and Boutry, 2000). With considering of its multiple physiological roles and high ATP consumption by plasma membrane H^+ATPases, these enzymes are tightly controlled at transcription, translation and enzymatic levels. A multigene family is encoding the plant plasma membrane H^+ATPase. Ten genes have been identified in A. thaliana, seven genes in tomato, five genes so far in Vicia faba, two genes in Oryza sativa and Zea mays and one gene in Phaseolus vulgaris. Some cells need more H^+ATPase, so in this way, the presence of H^+ATPase in particular plant tissues or in cell types such as the root cap, root hairs and epidermis, guard cells and the transfer and stellar cells is more. It was shown that H^+ATPase gene expression in specific tissues was enhanced by salt stress, low hydritation potential, darkness, hormones such as auxin and metabolizable sugars (Morsomme and Boutry, 2000). So plant has these mechanisms that maximize or minimize salinity tolerance.

II.III. Absesic acid signaling pathway

Abscisic acid (ABA) has a main contribution in controlled physiological responses to salinity. Because of its quick accumulation in response to stresses and its role in inducing of many stress responses leading to plant survival, ABA is a stress hormone (Zhang et al., 2006). Plant cells sense hyper osmosis pressure of salt stress. After that cell volume decreases and this results in plasma membrane withdrawal from cell wall that would be sensed by stretch activated channels and transmembrane protein kinases, like two component histidine kinases and wall-associated kinases. These occurrences increase the biosynthesis of plant stress hormone Abscisic acid (Zhang et al., 2006; Jia et al., 2002; Xiong and Zhu, 2003; Kreps et al., 2002; Seki et al., 2001; Urao et al., 1999). In dried soil the origin of ABA in plant is firstly from roots and if drying process be extended ABA can also come from older leaves that relatively wilt sooner than younger leaves (Zhang and Davies, 1989). ABA in plant has an important contribution in controlling of water condition through guard cells, and also by initiation of genes encoding enzymes and proteins included in cellular dehydration tolerance. In all of the ABA-responsive genes, their promoter domain has an ABA-responsive element ABRE (PyACGTGGC where Py shows a pyrimidine base, C or T). When ABRE would be bounded with its corresponding bzip family of transcription factors, it can result in ABA-induced gene expression. As an example, in Arabidopsis the dehydration-responsive rd29B gene mediated by ABA has two necessary ABREs for its expression. Two bzip transcription factors, AREB1 and AREB2, are included in the ABA-mediated expression of rd29B via phosphorylation by an ABA activated protein kinase (Zhang et al., 2006). ABA has a role in reducing of ethylene production (ethylene as a growth inhibitor in stress). In the ABA redistribution in leaf and controlling of stomata, pH changes have an important role (Zhang et al., 2006; Luan, 2002; Zhu, 2002). Some of the ABA roles are listed below:

a) Salinity stress causes ABA accumulation (especially ABI1). The AtNHX1 promoter, including ABA responsive elements (ABRE), so the NHX1 gene encoding vacuole membrane Na^+/H^+ antiporter, is induced by both salinity and the ABA. Also ABA seems to control SOS pathway through ABA insensitive 2 (ABI2) protein phosphatase 2C. ABI2 interacts with SOS2 and negatively control ion homeostasis either by inhibiting SOS2 kinase activity or the activities of SOS2 targets in Na^+/H^+ transporter in the plasma membrane. ABI2 interacts with the protein phosphatase interaction (PPI) motif of SOS2 (Ohta et al., 2003; Shi and Zhu, 2002).
b) ABA and osmotic stress through *OSM1* gene in the vegetative parts of plants induces late-embryogenesis-abundant (LEA) proteins leading to dehydration tolerance. These LEA-type proteins are encoded by RD (responsive to dehydration), ERD (early responsive to dehydration), KIN (cold inducible), COR (cold regulated), and RAB (responsive to ABA) genes in different plant species. Different plant species with different stress tolerance have different accumulation levels of these proteins. Transgenic rice plants over expressing of a barley LEA gene, HVA1, show better stress tolerance. Promoters of LEA genes contain dehydration responsive elements/C-Repeat (DRE/CRT), ABA-responsive elements (ABREs), and/or MYB/MYC recognition elements. The DRE/CRT elements control gene expression in response to dehydration (salt, drought, and cold stresses); while, ABRE and MYB/MYC elements are controlling gene expression by ABA in abiotic stresses (Shinozaki and Yamaguchi Shinozaki, 2000; Mohamed et al., 2007; Xu et al., 1996).
c) ABA also controls osmolyte biosynthesis in plants in salinity stress. For an example, Osmotic stress-induced ABA accumulation has a role in controlling of *P5CS* gene involved in proline biosynthesis (Xiong et al., 2001).
d) The second messengers (like Ca^{2+}, calmodulin, IP3/DG) and protein kinases or phosphatase (such as pKC, CDPKs, MAPKs, HTK, etc.) are main signal components inducing different plant responses to biotic and abiotic stimuli. Ca^{2+} also plays critical contribution in water or salt stress-induced ABA accumulation. Salt-stress/ABA induces Ca^{2+} signals are at least partially transduced through calcium-dependent protein kinases (CDPKs). Transient expression analyses protoplasts have shown that an increase in cytosolic Ca^{2+} concentration activates CDPKs, which in turn induce the stress responsive HVA1 promoter. Transgenic Overexpressing OsCDPK7 results in increase induction of an LEA-protein gene (RAB16A) and salt/drought tolerance. While, transgenic suppression of OsCDPK7 results in hypersensitivity to salt/drought stress (Xiong et al., 2002; Saijo et al., 2000).
e) Salt stress and ABA induce enhanced production of H_2O_2 acting as a second messenger to control antioxidant defense genes in abiotic stresses. ABA-elicited H_2O_2 production is negatively controlled by ABI2 protein in guard cells (Zhang et al., 2006; Hernandez et al., 2001; Guan et al., 2000; Pei et al., 2000).
f) H extrusion into the xylem is happened by the addition of ABA to plants, that this would motivate Na^+/H^+ antiporter in the xylem parenchyma plasma membrane and its result is less Na entering into the xylem and aerial organs (Clarkson and Hanson, 1986).

The controlling of the ABA Production should be perceptively and quickly, so that started with the stress to keep away from any plant growth and functions holding back under normal situation. The second previous stipulation is that the ABA should be quickly broken down and deactivated since stress is obviated, so that normal plant growth and functions can begin again (Zhang et al., 2006).

Figure 2 is trying to summarily show ion homeostasis mechanisms.

III. Accumulation of compatible solutes

It is necessary for plants to keep internal water potential lower than soil water potential to keep turgor and water absorb for growth, and in this way the necessities is osmotic raising, either by soil solute absorb or by metabolically compatible solutes synthesis (or also named as osmoprotectants). Plants by synthesis and accumulating of various compatible osmolytes in cytosol, decreasing osmotic potential to keep water absorption from saline soil solutions and limit salt absorption (Shahbaz and Ashraf, 2013; Deivanai et al., 2011; Ashraf and Foolad, 2007; Vinocur and Altman, 2005; Ashraf and Harris, 2004).The osmolytes work to regulate vacuolar and cytoplasmic volume, which in turn is significant to turgor keeping of the salinity cell exposure. Furthermore, these substances have important roles in supporting of different cellular structures and necessary proteins preserving normal physiological activity and also in maintenance of protein and ribosome structures from harmful effects of cytoplasmic Na. Until now, any kind of substances produced at high levels in stress situation has been recognized as osmolytes, that are produced by rate restricting enzymes (Fu et al., 2011; Turkan and Demiral, 2009; Ashraf and Foolad, 2007: Tester and Davenport, 2003).

Low molecular weight, neutral, very soluble compounds, not poisonous at high concentrations, and the one that just by itself can produce salinity toleration, are the features of Compatible solutes (Tester and Davenport, 2003). For example, transgenic wheat with the ability of the sugar alcohol mannitol synthesis can decrease the cytoplasm osmotic potential and increase the water absorption in water deficiency (Tester and Bacic, 2005). The main cheap solutes in saline soil are Na and Cl (compartmentation them into the vacuole), while poisonous in cytosol. Compatible solutes are not poisonous, but they are energetically very expensive. Anyway, many plants use organic osmolytes to tolerate osmotic stress (Chinnusamy et al., 2005; Tester and Davenport, 2003). A signaling cascade Mitogen Activated Protein Kinase (MAPK) pathway controls the biosynthesis of osmolyte (Zhu, 2002). Also ABA controls the biosynthesis of osmolyte called chaperons in plants in salinity (Xiong et al., 2001). The present compatible osmolytes in higher plants, including: low molecular weight sugars (like sucrose, maltose and trehalose), organic acids, polyols (like mannitol, glycerol, sorbitol, cyclic (cyclitols) forms, ononitol and pinitol), and nitrogen having substances such as amino acids (like proline), amides, amino acids, ectoine (1,4,5,6-tetrahydro-2-methyl- 4-carboxylpyrimidine), soluble proteins (like osmotin and LEA proteins) and quaternary ammonium compounds (QACs like glycine betaine, alaninebetaine, prolinebetaine, choline O sulfate, hydroxyprolinebetaine and pipecolatebetaine). Dehydration responsive elements (DREs) and ABA-responsive elements (ABREs) are contained in the promoter zones of these genes, that very possible are firstly responsive to osmotic effect and secondly Na specific effect and different proteins binding to these elements (Turkan and Demiral, 2009; Mohamed et al., 2007; Liu et al., 1998).

In here, it is worthy to say that a recent article has reported that the external application of sulfur metabolites (Amino acids (cysteine and methionine), Vitamins (biotin and thiamine), Thioredoxin system, Glutathione lipoic acid and Glucosinolats) can enhance the salinity tolerance of plants. Sulfur incorporates in cellular structure and signaling molecules against (Khan et al., 2014). Sometimes compatible osmolytes have different effects in the way of salinity tolerance. Artificial over production of compatible osmolytes in transgenic plants such as *Arabidopsis*, rice, wheat, and *Brassica* has been demonstrated to increase stress tolerance measured by germination, seedling growth, survival, recovery, photosystem II yield, and seed production in very salinity and osmotic stresses and the tolerance was associated with compatible osmolytes osmoprotectant effect instead of their role in osmotic adjustment (Sadat Noori et al., 2011b; Ashraf and Harris, 2013; Chinnusamy et al., 2005), these plants can keep normal K/Na ratios and this ion homeostasis was due to direct controlling of ion transporters or cellular integrity holding by saving of membranes and proteins from oxidative damage (Rai et al., 2011; Ashraf and Foolad, 2007; Chinnusamy et al., 2005). Some genes with different originations have identified that has a role in producing of compatible solutes to cause tolerance, some of them are listed below:

a) *mt1D* (mannitol-1-phosphate dehydrogenase) gene of E. coli (Abebe et al., 2003)
b) *Stpd1* (sorbitol-6-phosphate dehydrogenase) gene of apple (Gao et al., 2001)
c) *CodA* (choline oxidase) gene of Arthrobacter globiformis (Mohanty et al., 2002); choline dehydrogenase (*betA*) gene of E. coli (Holmstrom et al., 2000); betaine aldehyde dehydrogenase (*betB*) gene of E. coli (Holmstrom et al., 2000); *betaine aldehyde dehydrogenase (BADH*) gene of Atriplex hortensis (Guo et al., 2000); *peroxisomal BADH* gene of barley (Kishitani et al., 2000)
d) *P5CS* pyrroline-5-carboxylate synthetase gene of Vigna aconitifolia L. (Kishor et al., 1995); Antisense *proline dehydrogenase*
e) *otsA* (Trehalose-6-phosphate synthase) gene of E. coli; *otsB* (Trehalose 6-phosphate phosphatase) bifunctional fusion gene of E. coli (Nanjo et al., 1999)

Proline can be gathered in plants in larger quantities than other amino acids in salt stress (Fahramand et al., 2014; Sadat Noori et al., 2011b; Deivanai et al., 2011; Ashrafijou et al., 2010; Ashraf and Foolad, 2007). Osmotic stress-induced ABA accumulation controls *P5CS* gene producing proline. Beside of its role in osmotic adjustment firstly as a cytoplasmic solute, Proline brings about the expression of salt stress responsive genes containing proline responsive elements (*PRE*, ACTCAT) in their promoters (Satoh et al., 2002; Xiong et al., 2001). Proline is also believed to be considered as an osmoprotectant and as a hydroxyl radical scavenger. There are some reports about that Proline play a role in protecting enzymes from denaturation, stabilizing the machinery of protein synthesis, controlling the cytosolic acidity, increasing water binding capacity, and working as a carbon and nitrogen additional supply. So, these organic osmolytes are called as osmoprotectants (Sadat Noori et al., 2011b; Ashrafijou et al., 2010; Ashraf and Foolad, 2007; Vinocur and Altman, 2005; Su and Wu, 2004; Ashraf and Harris, 2004; Chen and Murata, 2000; Bohnert and Jensen, 1996). Glycinebetaine (GB) is another effective compatible solute and its accumulation is highly accompanied with plant development in saline and dry conditions. In chloroplasts and plastids of many halotolerant plants can find GB. One of the best examples in this way is cyanobacteria extremely tolerant to salt stress that biosynthesize and collects GB in their cytoplasm. Even GB outer implementation can make better the some species tolerance (Chen and Murata, 2008; Ashraf and Foolad, 2007). The structure and work of many macromolecules (for example, oxygen-evolving photosystem II protein pigment complex) could be stabilized by glycinebetaine (Goela et al., 2011). In very saline situations to stabilize of membrane, enzymes and protein complexes, Glycinebetaine is more effective than the other compatible solutes (Gorham, 2010). Activating or stabilizing ROS scavenging enzymes and repressing the ROS production could be done by GB (Chen and Murata, 2008). One of the most successful genetic engineering about glycinebetaine biosynthesis leading to the tolerant plants has obtained by introducing a bacterial codA gene encoding choline oxidase to Arabidopsis, Brassica, rice, maize, tomato and potato (Goela et al., 2011; Ashraf and Foolad, 2007; Vinocur and Altman, 2005; Li et al., 2003). Osmotin with its two forms, as a compatible solute is a bunch of cationic proteins (differ in Point of Isoelectric, in molecular weight and water solubility). Majorly in the vacuoles of tolerant cells to NaCl, Osmotin accumulates (Singh et al., 1987). Osmotin is grouped in PR-5 type of pathogenic related proteins of tobacco. Some causes, including ABA, ethylene, tobacco mosaic virus infection, salinity, desiccation, and wounding in both cultured cells, whole plants of tobacco, salicylic acid, fungal infection, drought, UV light, cold and auxinthe can control synthesis and accumulation of osmotin mRNA. Osmotin accumulation is connected with ABA level in the cell. Quickly after water potential rising in the environment, translation of osmotin mRNA starts. After NaCl stress obviating, the collected osmotin persist for 40 generations (Sadat Noori and Sokhansanj, 2008; Singh et al., 1989; Singh et al., 1987). Until now there are some articles on salt tolerance producing in crops like strawberry, tobacco and tomato by osmotin gene introducing (Husaini and Abdin, 2008). Trehalose, a so called enigmatic disaccharide of glucose (a-D-glucopyranosyl a-D-glucopyranoside) can improve the effects of salinity stress, high/low temperature and oxidative stresses. Trehalose biosynthesis has been to able make a salt tolerance in transgenic tobacco, tomato, potato and rice. One of the recognized genes for trehalose production is TPS1 gene with the origination of yeast (Cortina and Culianez Macia, 2005; Garg et al., 2002).

IV. Transcription factors

Stresses like Salinity, drought and extreme temperature are causing negative effects on plants. The signal of these stresses (dehydration and/or frost) from out of cytosol is transferred to nucleus through MAPKs and Protein Kinases. In response to various stresses numerous of genes are upregulated and physiological response to stresses is due to the changes in these genes. MAPK is a Serine/threonine protein kinase that for gene expression, phosphorilating a range of substrates. The message of activated MAPK transferred into the nucleus, phosphorylate and activate transcription factors and ultimately regulate plant stress response gene (Jenks et al., 2007; Chinnusamy et al., 2005: Chen et al., 2002; Xiong et al., 2002; Liu et al., 1998).

Transcription factors are sequence specific DNA binding proteins activating and/or repressing the transcription process of related genes to stresses (Wei et al., 2000). Some of these related genes are acting in many stresses while some can be specific to a special stress, and be activated based on tissue, developmental stage, and the extremity of stress (Jenks et al., 2007; Bohnert et al., 2001). The products of these genes can be classified into two groups:

a) Those including in directly acts to save cells from the harmful effects of environmental stresses (such as necessary enzymes for biosynthesis of various osmoprotectants, LEA proteins, chaperones, and detoxification enzymes) (Kasuga et al., 1999).
b) Those including in gene expression and signal (transcription factors such as DREB, bZIP, MYC and MYB; protein kinases and enzymes in phosphoinositide metabolism and producer of ABA) (Shinozaki and Yamaguchi Shinozaki, 1997; Bray, 1997).

The activity of a particular series of transcription factors and their binding to specific sequences in promoter regions of target genes are necessary in the way of upregulation of the related genes to stresses (Jenks et al., 2007; Chen et al., 2002; Xiong et al., 2002; Bohnert et al., 2001; Liu et al., 1998). There are two pathways for induction of these genes: mostly an ABA independent and minorly an ABA dependent pathway (Wei et al., 2000). Also, there is a report on the effects of calcium for the stress-responsive gene induction (Jenks et al., 2007).

The major transcription factor families that are induced by the abiotic stresses are listed below:

a) *DREB1A* TF includes dehydration-responsive elements (DRE's)
b) AP2/EREBP TF (Apetala 2/ethylene responsive element binding factor) family
c) bZIP TF family
d) MYB TF family
e) bHLH TF family, such as AtMYC2 and ICE1
f) NAC TF family, such as RD26/ANAC072, ANAC019 and ANAC055
g) Cys2His2 zinc-finger TF family, such as ZAT12
h) Homeodomain TF family, such as HOS9
i) Cys2Cys2 zinc-finger; WRKY; HB
j) HSF functioning in stress-inducible gene expression (Jenks et al., 2007).

The *DREB1A* transcription factor is particularly to *DRE* elements and induces the stress tolerance gene expression. Over expression of genes encoding these proteins can induce high gene expression leading to stress tolerance, but reduced growth is inevitable event even in the condition without stress, for example minimum 12 genes in Arabidopsis can be activated by *DREB1A*, consequently plant would be tolerant and dwarfism. Therefore, such genes should be used with stress inducible promoter (*rd29A*), till plants in normal condition seem normal and in stress condition shows stress tolerance. Sometimes these transcription factors may have similar functions in plants, for example a stress inducible DREB1A responsive gene like *rd29A*, and some genes encoding LEA protein like *cor47/rd17* and *erd10* genes encoding similar protein. LEA (embryogenesis abundant protein) proteins appear during embryo maturation and seeds desiccation, and are also induced by drought, salt, and cold stresses in the vegetative tissues of plants (Dure et al., 1989; Ingram and Bartels, 1996).

Increasing in LEA proteins in plants is associated with dehydration tolerance. Over expression of LEA in transgenic rice has proved the tolerance to salt stress (Xu et al., 1996). The *cor15a* gene as a one that is induced by LEA encodes a protein aimed to the chloroplasts stromal compartment, enhances the freezing tolerance of *Arabidopsis* leaf protoplasts. (Villalobos et al., 2004; Seki et al., 2001; Shinozaki and Yamaguchi Shinozaki, 2000; Artus et al., 1996; Yamaguchi Shinozaki and Shinozaki, 1993; Lin and Thomashow, 1992; Dure et al., 1989). AP2/EREBP (ethylene responsive element binding protein), a type of transcription factors, famously present in plants. In Arabidopsis, there are 145 members of AP2/EREBP, which including 5 subfamilies of AP2, RAV, DREB, AL079349 and ERF. The ERF (Ethylene responsive factor) subfamily has 65 genes that mostly are including in signal conductions in both biotic and abiotic stresses and control downstream gene expression. AP2/ERF class a subfamily thereof, the dehydration response element binding protein /C-repeat binding factor (DREB/CBF) are involved in ABA independent control. DREB transcription factors activate DRE or C-repeat containing genes (genes such as DREB1A/CBF3, DREB1C/CBF2, rice DREB1/CBF homolog, OsDREB1A and *Brassica* DREB1/CBF homologs, BNCBF5 and 17, DREB2A). The bZIP family of TF is another class of TF involved in drought response. Within the bZIP family of TFs, some subfamilies were identified. One subgroup consists of TFs that bind to the conserved cis acting sequences known as ABA responsive elements (ABRE); these TFs are hence termed ABRE binding factors (ABFs) (genes such as AREB1). The MYB TF (such as AtMYB2, AtMYB60 and HOS10) is one member of the transcription factor family, AtMYB60, an R2R3-MYB guard-cell specific TF, is down regulated during drought stress, since knockout of AtMYB60 leaded in a reduction of stomatal opening, and therefore reduced wilting in dehydration stress. ABA sensitive bZIP and MYC/MYB transcription factors are directly connected to induction of stress sensitive genes such as rd22 and rd29B. Another level of control of stomatal opening is stability and processing of mRNAs of ABA responsive genes (Yan et al., 2008; Jenks et al., 2007; Kim et al., 2003).

Conclusion

The first step to solve the salinity problem is identifying and ranking of saline areas. After that and making sure traditional methods are not applicable, to overcome the salinity problem and continuous production of food, it is recommended plant breeders use the best available strategies like conventional breeding, marker assisted selection and genetic engineering to develop salinity tolerant crops. Anyway to make a better use of new technologies like gene engineering a complete and deeper understanding of molecular and cellular basis of salt stress tolerance mechanisms is necessary, in this way please study this article precisely at first.

References

Abebe T, Guenzi AC, Martin B, Cushman JC (2003) Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. Plant Physiol. 131: 1748–1755.

Afzal M, Ahmad A, Alderfasi AA, Ghoneim A, Saqib M (2014) Physiological tolerance and cation accumulation of different genotypes of Capsicum annum under varying salinity stress. P Int Acad Ecol Environ Sci. 4 (1): 39-49.

Allbed A, Kumar L (2013) Soil Salinity Mapping and Monitoring in Arid and Semi-Arid Regions Using Remote Sensing Technology: A Review. Adv Remote Sensing. 2: 373-385.

Amtmann A, Sanders D (1999) Mechanisms of Na+ uptake by plant cells. Adv Bot Res. 29: 75–112.

An R, Chen QJ, Chai MF, Lu PL, Su Z, Qin ZX, Chen J, Wang XC (2007) AtNHX8, a member of the monovalent cation:proton antiporter-1 family in Arabidopsis thaliana, encodes a putative Li/H antiporter. Plant J. 49: 718–728.

Apse MP, Aharon GS, Sneddon WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na+/H+ antiport in Arabidopsis. Science. 285: 1256-1258.

Apse MP, Blumwald E (2007) Na+ transport in plants, FEBS Lett. 581: 2247– 2254.

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol. 55: 373–399.

Artus NN, Uemura M, Steponkus PL, Gilmour SJ, Lin C, Thomashow MF (1996) Constitutive expression of the cold regulated Aradidopsis thaliana COR15a gene affects both chloroplast and protoplast freezing tolerance. P Natl Acad Sci. 93: 13404–13409.

Aslam R, Bostan N, Amen N, Maria M, Safdar W (2011) A critical review on halophytes: Salt tolerant plants. J Med Plants Res. 5 (33): 7108-7118.

Ashraf M (2009) Biotechnological approach of improving plant salt tolerance using antioxidants as markers. Biotechnol Adv. 27: 84–93.

Ashraf M, Harris PJC (2004) Potential biochemical indicators of salinity tolerance in plants. Plant Sci. 166: 3–16.

Ashraf M, Foolad MR (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot. 59: 206–216.

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: An overview. Photosynthetica. 51 (2): 163-190.

Ashrafijou M, Sadat Noori SA, Izadi Darbandi A, Saghafi S (2010) Effect of salinity and radiation on proline accumulation in seeds of canola (Brassica napus L.). Plant Soil Environ. 56 (7): 312-317.

Ashraf M, Mcneilly T (2004) Salinity tolerance in Brassica oilseeds. Crc Cr Rev Plant Sci. 23 (2): 157-174.

Bahmani K, Izadi Darbandi A, Sadat Noori SA, Jafari AA, Moradi N (2012a) Determination of interrelationships among phenotypic traits of Iranian fennel (Foeniculum vulgare Mill.) using correlation, stepwise regression and path analyses. J Essent Oil Bear Pl. 15 (3): 424-444.

Bahmani K, Izadi Darbandi A, Jafari AA, Sadat Noori SA, Farajpour M (2012b) Assessment of Genetic Diversity in Iranian Fennels Using ISSR Markers. J Agr Sc. 4 (9): 79-84.

Bahmani K, Izadi Darbandi A, Sadat Noori SA, Jafari AA (2013) Assessment of the Genetic Diversity in Iranian Fennels by RAPD Markers. J Herbs Spices Med Plants. 19: 275–285.

Bandeh Hagh A, Toorchi M, Mohammadi A, Chaparzadeh N, Salekdeh G H, Kazemnia H (2008) Growth and osmotic adjustment of canola genotypes in response to salinity. J Food Agric Environ. 6 (2): 201-208.

Batelli G, Verslues PE, Agius F, Qiu Q, Fujii H, Pan S, Schumaker KS, Grillo S, Zhu JK (2007) Interaction of SOS2 with Nucleoside Diphosphate Kinase 2 and Catalases Reveals a Point of Connection between Salt Stress and H2O2 Signaling in Arabidopsis thaliana. Mol Cell Biol. 27: 7781–7790.

Batistic O, Kudla J (2004) Integration and channeling of calcium signaling through the CBL calcium sensor/CIPK protein kinase network. Planta. 219: 915–924.

Batlle DC, Kurtzman NA (1985) Renal regulation of acid-base homeostasis: an integrated response. In The Kidney: Physiology and Pathophysiology, D. W. Seldin and G. Giebisch, editors. Raven Press, New York. 1539-1565.

Batool N, Shahzad A, Ilyas N, Noor T (2014) Plants and Salt stress. Int J Agri Crop Sci. 7 (9): 582-589.

Bohnert HJ, RG Jensen (1996) Strategies for engineering water stress tolerance in plants. Trends Biotechnol. 14:89–97.

Bohnert HJ, Ayoubi P, Borchert C, Bressan RA, Burnap RL, Cushman J, et al (2001) A genomics approach toward salt stress tolerance. Plant Physiol Biotech. 39: 295-311.

Bray EA (1997) Plant responses to water deficit. Trends Plant Sci. 2: 48–54.

Brett CL, Donowitz M, Rao R (2005) Evolutionary origins of eukaryotic sodium/proton exchangers. Am J Physiol Cell Physiol. 288: 223–239.

Brumos J, Colmenero Flores JM, Conesa A, Izquierdo P, Sanchez G, Iglesias DJ, Lopez Climent MF, Gomez Cadenas A, Talon M (2009) Membrane transporters and carbon metabolism implicated in chloride homeostasis differentiate salt stress responses in tolerant and sensitive Citrus rootstocks. Springer Verlag. Funct Integr Genomics.

Cheeseman JM (1982) Pump leak sodium fluxes in low salt corn roots. J Membrane Biol. 70: 157-164.

Chen THH, Murata N (2000) Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. Curr Opin Plant Biol. 5: 250–257.

Chen THH, Murata N (2008) Glycinebetaine: an effective protectant against abiotic stress in plants. Trends Plant Sci. 13 (9): 499-505.

Cheng NH, Pittman JK, Zhu JK, Hirschi KD (2004) The protein kinase SOS2 activates the Arabidopsis H+/Ca2+ antiporter CAX1 to integrate calcium transport and salt tolerance. J Biol Chem. 279: 2922–2926.

Chen W, et al (2002) Expression profile matrix of arabidopsis transcription factor genes suggests their putative functions in response to environmental stresses. Plant cell. 14: 559-474.

Chinnusamy V, Jagendorf A, Zhu JK (2005) Understanding and Improving Salt Tolerance in Plants. Crop Sci. 45: 437–448.

Cortina C, Culianez Macia FA (2005) Tomato abiotic stress enhanced tolerance by trehalose biosynthesis. Plant Sci. 169: 75–82.

Clarkson DT, Hanson JB (1986) Proton fluxes and the activity of a stelar proton pump in onion roots. J Exp Bot. 37: 1136-1150.

Cramer GR (2002) Sodium calcium interactions under salinity stress. In: Salinity. Environment-Plants-Molecules.. A. Lauchli and U. Luttge (Eds) . Kluwer Academic Publishers, Dordrecht. 205–227

Davenport RJ, Tester M (2000) A weakly voltage dependent nonselective cation channel mediates toxic sodium influx in wheat. Plant Physiol. 122: 823-834.

Deivanai S, Xavier R, Vinod V, Timalata K, Lim OF (2011) Role of Exogenous Proline in Ameliorating Salt Stress at Early Stage in Two Rice Cultivars. J Stress Physiol Biochem. 7 (4): 157-174.

Demidehik V, Davenport RJ, Tester M (2002) Non selective cation channels. Annu Rev Plant Physiol Plant Mol Biol. 53: 67-107.

Demidehik V, Tester M (2002) Sodium fluxes through non selective cation channels in the plasma membrane of protoplalsts from Arabidopsis taliana roots. Plant Physiol. 128: 379-387.

Dorani Uliaie E, Ghareyazie B, Farsi M, Kogel KH, Imani J (2012) Improved salt tolerance in canola (Brasica napus) plants by overexpression of Arabidopsis Na+/H+ antiporter gene AtNHX1. J Plant Mol Breed. 1 (1): 34-42.

Doucet A, Marcy S (1987) Characterization of K-ATPase activity in distal nephron: stimulation by potassium depletion. Am J Physiol. 253: 418-423.

Dure L, Crouch M, Harada J, David Ho TH, Mundy J, Quatrano R, Thomas T, Sung ZR (1989) Common amino acid sequence domains among the LEA proteins of higher plants. Plant Mol Biol. 12: 475–486.

Ebrahimi R, Bhatla SC (2012) Ion distribution measured by electron probe X-ray microanalysis in apoplastic and symplastic pathways in root cells in sunflower plants grown in saline medium. J Biosciences. 37 (4): 713–721.

Eiam Ong S, Kurtzman NA, Sabatini S (1993) Regulation of Collecting Tubule Adenosine Triphosphatases by Aldosterone and Potassium. J Clin Invest. 91: 2385-2392.

Eltelib HA, Fujikawa Y, Esaka M (2012) Overexpression of the acerola (Malpighia glabra) monodehydroascorbate reductase gene in transgenic tobacco plants results in increased ascorbate levels and enhanced tolerance to salt stress. S Afr J Bot. 78: 295–301.

Essah PA, Davenport R, Tester M (2003) Sodium influx and accumulation in Arabidopsis. Plant Physiol 133: 307–318.

Ezlit YD, Smith RJ, Raine SR (2010) A review of salinity and sodicity in irrigation. CRC Irrig Futures Matters Series. 1 (10): 5.

Fahramand M, Mahmoody M, Keykha A, Noori M, Rigi K (2014) Influence of abiotic stress on proline, Photosynthetic enzymes and growth. Int Res J Appl Basic Sci. 8 (3): 257-265.

Flowers TJ, Troke PF, Yeo AR (1977) The mechanisms of salt tolerance in halophytes. Annu Rev Plant Physiol. 28: 89-121.

Flowers TJ, Hajibagheri MA, Clipson NJW (1986) Halophytes. Q Rev Biol. 61: 313–336

Flower TJ, Yeo AR (1988) Ion relation of salt tolerance. In: Baker, D, and Halls, J. solute transport in plant cells and tissues. Harlow; longman. 392-416.

Foolad MR (2004) Recent advances in genetics of salt tolerance in tomato. Plant Cell Tiss Org. 76: 101-119.

Foyer CH, Noctor G (2005) Oxidant and antioxidant signalling in plants: a reevaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ. 28: 1056–1071.

Fu XZ, Ullah Khan E, Hu SS, Fan QJ, Liu JH (2011) Overexpression of the betaine aldehyde dehydrogenase gene from Atriplex hortensis enhances salt tolerance in the transgenic trifoliate orange (Poncirus trifoliata L. Raf.). Environ Exp Bot. 74: 106–113.

Fukuda A, Nakamura A, Tagiri A, Tanaka H, Miyao A, Hirochika H, Tanaka Y (2004) Function, Intracellular Localization and the Importance in Salt Tolerance of a Vacuolar Na+/H+ antiporter from Rice. Plant Cell Physiol. 45 (2): 146-159.

Garg LC, Narang N (1988) Ouabain insensitive K adenosine triphosphatase in distal nephron segments of the rabbit. J Clin Invest. 81:1204-1208.

Garg LC, Narang N (1990) Effects of low potassium diet on NEMsensitive ATPase in the distal nephron segment. Renal Physiol. J Biochem. 13: 129-136.

Garg AK, Kim JK, Owens TG, Ranwala AP, Choi YD, Kochian LV, Wu RJ (2002) Trehalose accumulation in rice plants confers high tolerances levels to different abiotic stresses. P Natl Acad Sci. 99: 15898-15903.

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-phos- phate dehydrogenase. Plant Sci. 160: 837–845.

Gaxiola RA, Li J, Undurraga S, Dang V, Allen GJ, Alper SL, Fink GR (2001) Drought and salt tolerant plants result from overexpression of the AVP1 H pump. P Natl Acad Sci. 98: 11444–11449.

Gilmascarell R, Lopezcoronado JM, Belles JM, Serrano R, Rodrigue PL (1999) The Arabidopsis HAL2-like gene family induces a novel sodium sensitive phosphatase. Plant J. 17: 373-383.

Glenn EP, Brown JJ, Blumward E (1999) Salt tolerance and crop potential of halophytes. Crc Cr Rev Plant Sci. 18: 227-255.

Gluck S, Al-Awqati Q (1984) An electrogenic proton-translocating adenosine triphosphatase from bovine kidney medulla. J Clin Invest. 73: 1704-1710.

Goela D, Singha AK, Yadava V, Babbarb SB, Muratac N, Bansala KC (2011) Transformation of tomato with a bacterial codA gene enhances tolerance to salt and water stresses. J Plant Physiol. 168: 1286–1294.

Gorham J, Wyn Jones RG, Bristol A (1990) Partial characterization of the trait for enhanced K-Na discrimination in the D genime of wheat. Planta. 180: 590-597.

Gorham J (2010) Betaines in higher plants biosynthesis and role in stress metabolism. In: Wallsgrove RM, editor. Amino acids and their derivatives in higher plants. Cambridge: Cambridge University Press. 173–204.

Guan LQM, Zhao J, Scandalios JG (2000) Cis elements and trans-factors that regulate expression of maize Cat1 antioxidant gene in response to ABA and osmotic stress: H2O2 is the likely intermediary signaling molecule for the response. Plant J. 22: 87–95.

Guo BH, Zhang YM, Li HJ, Du LQ, Li YX, Zhang JS, Chen SY, Zhu ZQ (2000) Transformation of wheat with a gene encoding for the betaine aldehyde dehydrogenase (BADH). Acta Bot Sin. 42: 279–283.

Guo Y, Qui QH, Wuintero FJ, Pardo JM, Ohta M, Zhang C, Schumaker KS, Zhu JK (2004) Transgenic Evaluation of Activated Mutant alleles of SOS2 Reveals a Critical Requirement for Its Kinase Activity and C-Terminal Regulatory Domain for Salt Tolerance in Arabidopsis thaliana. Plant Cell. 16: 435-449.

Halfter U, Ishitani M, Zhu JK (2000) The Arabidopsis SOS2 protein kinase physically interacts with and is activated by the calcium-binding protein SOS3. P Natl Acad Sci. 97: 3735-3740.

Heywood VH (2002) The conservation of genetic and chemical diversity in medicinal and aromatic plants. In: Şener, B. (Ed.), Biodiversity: Biomolecular Aspects of Biodiversity and Innovative Utilization. Kluwer Academic, Plenum Publishers, New York. 13-22.

Hernandez JA, Ferrer MA, Jimenez A, Barcelo AR, Sevilla F (2001) Antioxidant systems and O2 /H2O2 production in the apoplast of pea leaves. Its relationwith salt-induced necrotic lesions in minor veins. Plant Physiol. 127: 817–831.

Hille B (1992) Ionic Channels of Excitable Membranes (2nd edn), Sinauer.

Hirsch RE, Lewis BD, Spalding EP, Sussman MR (1998) A role for the AKT1 potassium channel in plantnutrition. Science. 280: 918–921

Holmstrom KO, Somersalo S, Mandal A, Palva TE, Welin B (2000) Improved tolerance to salinity and low temperature in trans genic tobacco producing glycine betaine. J Exp Bot. 51: 177–185.

Hossain Z, Mandal AKA, Datta SK, Biswas AK (2007) Development of NaCl tolerant line in Chrysanthemum morifolium Ramat. through shoot organogenesis of selected callus line. J Biotechnol. 129: 658–667.

Husaini AM, Abdin MZ (2008) Development of transgenic strawberry (Fragaria x ananassa Duch.) plants tolerant to salt stress. Plant Sci. 174: 446–455

Ingram J, Bartels D (1996) The molecular basis of dehydration tolerance in plants. Annu Rev Plant Biol. 47: 377–403.

Ismail A, Takeda S, Nick P (2014) Life and death under salt stress: same players, different timing. J Exp Bot. 65 (12): 2963–2979.

Izadi Darbandi A, Bahmani K (2011) Principal of Fennel cultivation and breeding. Tehran, Tamadon Pars.

Izadi Darbandi A, Bahmani K, Ramshini HA, Moradi N (2013) Heritability Estimates of Agronomic Traits and Essential Oil Content in Iranian Fennels. J Agr Sci Technol. 15: 1275-1283.

Jamil M, Rehman S, Rha ES (2014) Response of Growth, PSII Photochemistry and Chlorophyll Content to Salt Stress in Four Brassica Species. Life Sci J. 11 (3): 139-145.

Jenks MA, Hasegawa PM, Jain SM (2007) Advances in Molecular Breeding toward Drought and Salt Tolerant Crops: Plant Growth and Development Under Salinity Stress. Springer. 1–32.

Ji H, Pardo JM, Giorgia B, Van Oosten MJ, Bressan RA, Li X (2013) The Salt Overly Sensitive (SOS) pathway: established 1 and emerging roles. Mol Plant Adv. Access published January 25.

Jia W, Wang Y, Zhang S, Zhang J (2002) Salt stress induced ABA accumulation is more sensitively triggered in roots than in shoots. J Exp Bot. 53: 2201–2206.

Kasuga M, Liu Q, Miura S, Yamaguchi Shinozaki K, Shinozaki K (1999) Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. Nat Biotechnol. 17: 287-291.

Katiyar AS, Zhu J, Kim K, Agarwal M, Fu X, Huang A, Zhu JK (2006) The plasma membrane Na+/H+ antiporter SOS1 interacts with RCD1 and functions in oxidative stress tolerance in Arabdiopsis. P Natl Acad Sci. 103: 18816-18821.

Khadouri C, Cheval L, Marsy S, C Barlet Bas, Doucet A (1991) Characterization and control of proton ATPase along the nephron. Kidney Int. 40: 71-78.

Khan NA, Khan MIR, Asgher M, Fatma M, Masood A, Syeed S (2014) Salinity Tolerance in Plants: Revisiting the Role of Sulfur Metabolites. Plant Biochem Physiol. 2 (1).

Kim DY, Lee JE, Yi KW, Han SE, Kwon HB, Go SJ, Byun MO (2003) Expression pattern of potato (Solanum tuberosum) genes under cold stress by using cDNA microarray, Kor. J Genet. 25 (4): 345–352.

Kim BG, Waadt R, Cheong YH, Pandey GK, Dominguez Solis JR, Schultke S, Lee SC, Kudla J, Luan S (2007) The calcium sensor CBL10 mediates salt tolerance by regulating ion homeostasis in Arabidopsis. Plant J. 52: 473– 484.

Kishor PBK, Hong Z, Miao GH, Hu CAA, Verma DPS (1995) Overexpression of [delta]-pyrroline-5-carboxylate synthetase increases proline production and confers osmotolerance in trans genic plants. Plant Physiol. 108: 1387–1394.

Kishitani S, Takanami T, Suzuki M, Oikawa M, Yokoi S, Ishitani M, Alvarez Nakase AM, Takabe T, Takabe T (2000) Compatibility of glycinebetaine in rice plants: Evaluation using transgenic rice plants with a gene for peroxisomal betaine aldehyde dehydrogenase from barley. Plant Cell Environ. 23: 107–114.

Koohafkan P (2012) Water and Cereals in Drylands, The Food and Agriculture Organization of the United Nations and Earthscan.

Kopittke PM, Menzies NW (2004) Effect of pH on Na induced calcium deficiency. Plant Soil. 269: 119–129.

Kovtun Y, Chiu WL, Tena G, Sheen J (2000) Functional analysis of oxidative stress activated MAPK cascade in plants. P natl acad sci. 97: 2940-2945.

Kreps JA, Wu Y, Chang HS, Zhu T, Wang X, Harper JF (2002) Transcriptome changes for Arabidopsis in response to salt, osmotic, and cold stress. Plant Physiol. 130: 2129–2141.

Kudla J, Xu Q, Harter K, Gruissen W, Luan S (1999) Genes for calcineurin B-like proteins in Arabidopsis are differentially regulated by stress signals. P natl acad sci. 96: 4718-4723.

Kumar Parida A, Jha B (2010) Salt tolerance mechanisms in mangroves: a review. Trees. 24: 199–217.

Kurtzman NA (1990) Disorders of distal acidification. Kidney Int. 38: 720-727.

Laurie S, Feeney KA, Maathuis FJM, Heard PJ, Brown SJ, Leigh RA (2002) A role for HKT1 in sodium uptake by wheat roots. Plant J. 32: 139–149.

Leidi EO, Barragan V, Rubio L, El-Hamdaoui A, Ruiz MT, Cubero B, Fernandez JA, Bressan RA, Hasegawa PM, Quintero FJ, Pardo JM (2010) The AtNHX1 exchanger mediates potassium compartmentation in vacuoles of transgenic tomato. Plant J. 61: 495–506.

Li QL, Gao XR, Yu XH, Wang XZ, An LJ (2003) Molecular cloning and characterization of betaine aldehyde dehydrogenase gene from Suaeda liaotungensis and its use in improved tolerance to salinity in transgenic tobacco. Biotechnol Lett. 25: 1431-1436.

Lin C, Thomashow MF (1992) DNA sequence analysis of complementary DNA for cold-regulated *Arabidopsis* gene *corl5* and characterization of the COR15 polypeptide. Plant Physiol. 99: 519–525.

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchishinozaki K, Shinozaki K (1998) Two transcription factors DREB1 and DREB2 with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought and low temperature responsive gene expression respectively in Arabidopsis. Plant cell. 10: 1391-1406.

Liu J, Zhu JK (1992) Proline accumulation and salt stress induced gene expression in a salt hypersensitive mutant of Arabidopsis. Plant physiol. 114: 591-596.

Luan S (2002) Signalling drought in guard cells. Plant Cell Environ. 25: 229–237.

Luan S, Kudla J, Rodriguez MC, Yalovsky S, Gruissem W (2002) Calmodulins and Calcineurin B like Proteins. Plant Cell. 14: S389–S400.

MacDonald JD (1982) Effect of salinity stress on development of Phytophthora root rot of chrysanthemum. Phytopath. 72: 214–219.

Mahajan S, Tuteja N (2005) Archives of Biochemistry and Biophysics. Arch Biochem Biophys. 444: 139–158.

Mahajan S, Pandey GK, Tuteja N (2008) Calcium and salt stress signaling in plants: Shedding light on SOS pathway. Arch Biochem Biophys. 471: 146–158.

Marschner H (1995) Mineral Nutrition of Higher Plants, Academic Press.

Maser P, Eckelman B, Vaidyanathan R, Horie T, Fairbairn DJ, Kubo M, Yamagami M, Yamaguchi K, Nishimura M, Uozumi N et al (2002) Altered shoot/root NaR distribution and bifurcating salt sensitivity in Arabidopsis by genetic disruption of the NaR transporter AtHKT1. FEBS (Federation of European Biochemical Societies) Letters. 531: 157-161.

Mikami K, Kanesaki Y, Suzuki I, Murata N (2002) Membrane bound histidine kinase Hik33 is a bifunctional sensor involved in perception of osmostress and could in synechoccystis sp PCC 6803. Plant cell physiol. 43: S54-S54.

Mishra B, Singh RK, Jetly V (1998) Inheritance pattern of salinity tolerance in rice. J Genet Breed. 52: 325-331.

Mittler R (2002) Oxidative stress, anioxidants and stress tolerance. Trends Plant Sci. 7: 405-410.

Mittova V, Guy M, Tal M, Volokita M (2002) Response of the cultivated tomato and its wild salt-tolerant relative Lycopersicon pennellii to salt-dependent oxidative stress: increased activities of antioxidant enzymes in root plastids, Free Radic. Research. 36: 195–202.

Mohamed AA, Eichler Lobermann B, Schnug E (2007) Response of crops to salinity under Egyptian conditions: a review. Landbauforsch Volk. 2 (57):119-125.

Mohanty A, Kathuria H, Ferjani A, Sakamoto A, Mohanty P, Murata N, Tyagi A (2002) Transgenics of an elite indica rice variety Pusa Basmati 1 harbouring the codA gene are highly toler- ant to salt stress. Theor Appl Genet. 106: 51–57.

Mohsen AA, Ebrahim MKH, Ghoraba WFS (2014) Effect of salinity stress on Vicia faba productivity with respect to ascorbic acid treatment. Iran J Plant Physiol. 3 (3): 725-736.

Moon H, Lee B, Choi G, Shin D, Prasad DT, Lee O, Kwak SS, Kim DH, Nam J, Bahk J, Hong JC, Lee SY, Cho MJ, Lim CO, Yun DJ (2003) NDP kinase 2 interacts with two oxidative stress-activated MAPKs to regulate cellular redox state and enhances multiple stress tolerance in transgenic plants. P Natl Acad Sci.100: 358–363.

Morsomme P, Boutry M (2000) The plant plasma membrane H-ATPase: structure, function and regulation. Biochim Biophys Acta. 1465: 1-16.

Munns R (1993) Physiological processes limiting plant growth in saline soils some dogmas and hypotheses. Plant Cell Environ. 16: 15–24.

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ. 25 (2): 239–250.

Munns R, James RA, Lauchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot. 57: 1025–1043.

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol. 59: 651–681.

Murkute, A.A., Sharma, S. and Singh, S.K. 2005. Citrus in term of soil and water salinity: a review. J Sci Ind Res. 64: 393-402.

Nanjo T, Kobayashi TM, Yoshida Y, Kakubari Y, Yamaguchi Shinozaki K, Shinozaki K (1999) Antisense suppression of proline degradation improves tolerance to freezing and salinity in Arabidopsis thaliana. FEBS (Federation of European Biochemical Societies) Letters. 461: 205–210.

Nikolova MT, Ivancheva SV (2005) Quantitative flavonoid variations of Artemisia vulgaris L. and Veronica chamaedrys L. in relation to altitude and polluted environment. Acta Biol Szegediensis. 49: 29-32.

Noctor G, Foyer CH (1998) Ascorbate and glutathione: keeping active oxygen under control. Annu Rev Plant Phys. 49: 249–279.

Ohta M, Guo Y, Halfter U, Zhu JK (2003) A novel domain in the protein kinase SOS2 mediates interaction with the protein phosphatase 2C ABI2. P Natl Acad Sci. 100: 11771– 11776.

Pandolfi C, Mancuso S, Shabala S (2012) Physiology of acclimation to salinity stress in pea (Pisum sativum). Environ Exp Bot. 84: 44– 51.

Pardo JM, Reddy MP, Yang S, Maggio A, Huh GH, Matsumoto T, Coca M, Urzo MP, Koiwa H, Yun DJ, Watad A, Bressani RA, Hasegawa PM (1998) Stress signaling through Ca/calmodium dependent protein phosphatase calcineurin mediates salt adaption in plants. P natl acad sci. 96: 4718-4723.

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotox Environ Safe. 60: 324–349.

Parvaiz A, Satyawati S (2008) Salt stress and phytobiochemical responses of plants-a review. Plant Soil Environ. 54: 89–99.

Pei ZM, Murata Y, Benning G, Thomine S, Klusener B, Allen GJ, Grill E, Schroeder I (2000) Calcium channels activated by hydrogen peroxide mediate abscisic acid signaling in guard cells. Nature. 406: 731–734.

Perrenoud S (1990) Potassium and Plant Health, International Potash Institute, Basel.

Pilot G, Gaymard F, Mouline K, Cherel I, Sentenac H (2003) Regulated expression of Arabidopsis shaker KR channel genes involved in KR uptake and distribution in the plant. Plant Mol Biol. 51: 773-787.

Pitman MG, Lauchli A (2002) Global impact of salinity and agricultural ecosystems, in: salinity environment-plants molecules, Lauchli, A. and V. Luttge (Eds). Kluwer, Netherlands: 3-20.

Plaut Z, Edelstein M, Ben Hur M (2013) Overcoming Salinity Barriers to Crop Production UsingTraditional Methods. Crit Rev Plant Sci. 32: 250–291.

Plett DC, Moller IS (2010) Na+ transport in glycophytic plants: what we know and would like to know. Plant Cell Environ. 33: 612–626.

Polle A (2001) Dissecting the superoxide dismutase-ascorbate-glutathione-pathway in chloroplasts by metabolic modeling, Computer simulations as a step towards flux analysis. Plant Physiol. 126: 445-462.

Quan R, Lin H, Mendoza I, Zhang Y, Cao W, Yang Y, Shang M, Chen S, Pardo JM, Guo Y (2007) A putative calcium sensor, interacts with the protein kinase SOS2 to protect Arabidopsis shoots from salt stress. Plant Cell 19: 1415–1431.

Qui QS, Guo Y, Dietrich MA, Schumaker KS, Zhu JK (2002) regulation of SOS1, a plasma membrane Na+/H+ exchanger in Arabidopsis thaliana, by SOS2 and SOS3. P Natl Acad Sci. 99: 8436-8441.

Rai MK, Kalia RK, Singh R, Gangola MP, Dhawan AK (2011) Developing stress tolerant plants through in vitro selection-An overview of the recent progress. Environ Exp Bot. 71: 89–98.

Rameeh V (2013) Effect of Salinity Stress on Yield, Component Characters and Nutrient Compositions in Rapeseed (Brassica napus L.) Genotypes. Agri tropica subtrop. 46 (2): 58-63.

Rani CR, Reema C, Alka S, Singh PK (2012) Salt Tolerance of Sorghum bicolor Cultivars during Germination and Seedling Growth. Res J Rec Sci. 1 (3): 1-10.

Ratner A, Jacoby B (1976) Effect of K+, its counter anion, and pH on sodium efflux from barley root tips. J Exp Bot. 27: 843–852.

Richards L (1954) Diagnosis and Improvement of Saline and alkali Soils. Soil Sci. 78 (2): 154.

Roy SJ, Negrao S, Tester M (2014) Salt resistant crop plants. Curr Opin Biotech. 26: 115–124.

Roy C, Sengupta DN (2014) Effect of Short Term NaCl Stress on Cultivars of S. lycopersicum: A Comparative Biochemical Approach. J Stress Physiol Biochem. 10 (1): 59-81.

Rus A, Yokoi S, Sharkhuu A, Reddy M, Lee BH, Matsumoto TK, Koiwa H, Zhu JK, Bressan RA, Hasegawa PM (2001) AtHKT1 is a salt tolerance determinant that controls Na entry into plant roots. P Natl Acad Sci. 98: 14150-14155.

Sadat Noori SA, McNeilly T (1999) Assessment of variability in salt tolerance in diploid Aegilops spp. J Genet Breed. 183-188.

Sadat Noori SA, McNeilly T (2000) Assessment of variability in salt tolerance based on seedling growth in Triticum durum Desf. Genet Resour Crop Ev. 47: 285–291

Sadat Noori SA, Sokhansanj A (2004) Triple test cross analysis for genetic components of salinity tolerance in spring wheat. J Sci. 15 (1): 13-19.

Sadat Noori SA (2005) Assessment for salinity tolerance through intergeneric hybridisation: Triticum durum × Aegilops speltoides. Euphytica. 146: 149–155.

Sadat Noori SA, Harati M (2005) Breeding for Salt-Resistance Using Transgressive Segregation in Spring Wheat. J Sci. 16 (3): 217-222.

Sadat Noori SA, Roustaei A, Foghi B (2006) Variability of salt tolerance for eleven traits in bread wheat grown in different saline conditions. J Agron. 5 (1): 131-136.

Sadat Noori SA, Mottaghi S, Lotfifar O (2008) Salinity tolerance of maize in embryo and adult stage. Am Eur J Agri Environ Sci. 3 (5): 717-725.

Sadat Noori SA, Sokhansanj A (2008) Wheat Plants Containing an Osmotin Gene Show Enhanced Ability to Produce Roots at High NaCl Concentration. Russ J Plant Physiol. 55 (2): 256–258.

Sadat Noori SA, Ebrahimi M, Khazaei J, Khalaj H (2011a) Predicting yield of wheat genotypes at different salinity by artificial neural network. Afr J Agric Res. 6 (12): 2660-2675.

Sadat Noori SA, Ferdosizadeh L, Izadi Darbandi A, Mortazavian SMM, Saghafi S (2011b) Effects of Salinity and Laser Radiation on Proline Accumulation in Seeds of Spring Wheat. J Plant Physiol Breed. 1 (2): 11-20.

Saijo Y, Hata S, Kyozuka J, Shimamoto K, Izui K (2000) Over expression of a single Ca2+ dependent protein kinase confers both cold and salt/drought tolerance on rice plants. Plant J. 23: 319–327.

Sanders D, Brownlee C, Harper JF (1999) Communicating with calcium. Plant Cell. 11: 691–706.

Satoh R, Nakashima K, Seki M, Shinozaki K, Yamaguchi Shinozaki K (2002) ACTCAT, a novel cis-acting element for pralines and hypoosmolarity-responsive expression of the ProDH gene encoding proline dehydrogenase in Arabidopsis. Plant Physiol. 130: 709–719.

Schachtman D, Liu W (1999) Molecular pieces to the puzzle of the interaction between potassium and sodium uptake in plants. Trends Plant Sci. 4 (7): 281-287.

Seki M, Narusaka M, Abe H, Kasuga M, Yamaguchi Shinozaki K, Carninci P, Hayashizaki Y, Shinozaki K (2001) Monitoring the expression pattern of 1300 Arabidopsis genes under drought and cold stresses by using a full-length cDNA microarray. Plant Cell. 13: 61-72.

Shahbaz M, Ashraf M (2013) Improving Salinity Tolerance in Cereals. Crit Rev Plant Sci. 32: 237–249.

Shang G, Li Y, Hong Z, Cheng long L, Shao Z, Qing chang L (2012) Overexpression of SOS Genes Enhanced Salt Tolerance in Sweetpotato. J Integr Agr. 11 (3): 378-386.

Shannon MC (1998) Adaptation of plants to salinity. Adv Agron J. 60: 75–119.

Shao HB, Chu LY, Jaleel CA (2008) Water deficit stress-induced anatomical changes in higher plants. C R Biol. 331 (3): 215-25.

Shi H, Ishitani M, Kim C, Zhu JK (2000) The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative NaR/HR antiporter. P Natl Acad Sci. 97: 6896-6901.

Shi H (2002) Regulation of expression of the vacuolar NaR/HR antiporter gene AtNHX1 by salt stress and ABA. Plant Mol Biol. 50: 543-550.

Shi H, Quintero FJ, Pardo JM, Zhu JK (2002) The putative plasma membrane Na/H antiporter SOS1 controls long distance Na transport in plants. Plant Cell. 14: 465–477.

Shi H, Lee B, Wu SJ, Zhu JK (2003) Overexpression of a plasma membrane Na+/H+ antiporter gene improves salt tolerance in Arabidopsis thaliana. Nat Biotechnol. 21: 81–5.

Shinozaki K, Yamaguchi Shinozaki K (1997) Gene expression and signal transduction in water-stress response. Plant Physiol. 115: 327–334.

Shinozaki K, Yamaguchi Shinozaki Y (2000) Molecular responses to dehydration and low temperature: differences and cross talk between two stress signaling pathways. Plant Biol. 3: 217-223.

Singh NK, Hasegawa PM, Handa AK, Buckel S, Hermodson MA, Pfankoch E, Regnier FE, Bressan RA (1987) Characterization of OSM. Plant Physiol. 85: 529–536.

Singh NK, Nelson DE, Rosa PC, Bracker CE, Handa AK, Hasegawa PM, Bressan RA (1989) Osmotin: A Protein Associated with Osmotic Stress Adaptation in Plant Cells, Environmental Stress in Plants, Cherry, J.A., Ed., Heidelberg: Springer Verlag. 67–87.

Snapp SS, Shennan C, Bruggen AHC (1991) Effects of salinity on severity of infection by Phytophthora parasitica Dast., ion concentrations and growth of tomato, Lycopersicon esculentum Mill. New Phytol. 119: 275–284.

Storey R, Walker RR (1999) Citrus and salinity. Sci Hortic. 78: 39–81.

Su J, Wu R (2004) Stress inducible synthesis of proline in transgenic rice confers faster growth under stress conditions than that with constitutive synthesis. Plant Sci. 166: 941–948.

Tester M, Davenport R (2003) Na tolerance and Na transport in higher plants. Ann bot. 91: 503-527.

Tester M, Bacic A (2005) Abiotic Stress Tolerance in Grasses. From Model Plants to Crop Plants. Plant Physiol. 137: 791–793.

Tian N, Wang J, Xu ZQ (2011) Overexpression of Na+/H+ antiporter gene AtNHX1 from Arabidopsis thaliana improves the salt tolerance of kiwifruit (Actinidia deliciosa). S Afr J Bot. 77: 160–169.

Tunuturk M, Tuncturk R, Yildirim B, Ciftci V (2011) Effect of salinity stress on plant fresh weight and nutrient composition of some Canola (Brassica napus L.) cultivars. Afr J Biotech. 10 (10): 1827-1832.

Turkan I, Demiral T (2009) Recent developments in understanding salinity tolerance. Environ Exp Bot. 67: 2–9.

Tuteja N, Mahajan S (2007) Calcium signaling network in plants: an overview. Plant Signal Behav. 2: 79–85.

Urao T, Yakubov B, Satoh R, Yamaguchi shinozaki K, Seki M, Hirayama T, Shinozaki K (1999) A transmembrane hybrid type histidine in Arabidopsis functions as an osmosensor. Plant cell. 11: 1743-1754.

Venema K, Belver A, Marin Manzano MC, Rodríquez Rosales MP, Donaire JP (2003) A novel intracellular K+/H+ antiporter related to Na+/H+ antiporters is important for K+ ion homeostasis in plants. J Biol Chem. 278: 22453– 22459.

Villalobos MA, Bartels D, Iturriaga G (2004) Stress tolerance and glucose insensitive phenotypes in Arabidopsis overexpressing the CpMYB10 transcription factor gene. Plant Physiol. 135: 309-324.

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotech. 16: 123–132.

Vranova E, Inze D, Van Breusegem F (2002) Signal transduction during oxidative stress. J Exp Bot. 53: 1227–1236.

Volkmar KM, Hu Y, Steppuhn H (1998) Physiological responses of plants to salinity: A review. Can J Plant Sci. 78: 19-27.

Wei JZ, Tirajoph A, Effendy J, Plant AJ (2000) Characterization of salt induced changes in gene expression in tomato roots and the role played by absesic acid. Plant Sci. 159: 133-148.

White PJ, Broadley MR (2001) Chloride in Soils and its Uptake and Movement within the Plant: A Review. Ann Bot. 88 (6): 967-988.

Wu SJ, Ding L, Zhu JK (1996) SOS1, a genetic locus essential for salt tolerance and potassium acquisition. Plant Cell. 8:617–27.

Xiong L, Ishitani M, Lee H, Zhu JK (2001) The Arabidopsis LOS5/ABA3 locus encodes a molybdenum cofactor sulfurase and modulates cold stress and osmotic stress responsive gene expression. Plant Cell. 13: 2063–2083.

Xiong I, Schumaker KS, Zhu JK (2002) Cell signaling during cold, drought, and salt stress. Plant cell. (supplement 2002): 165-183.

Xiong L, Yang Y (2003) Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid inducible mitogen activated protein kinase. Plant Cell. 15:745–759.

Xiong L, Zhu JK (2003) Regulation of abscisic acid biosynthe sis. Plant Physiol. 133:29–36.

Xu D, Duan X, Wang B, Hong B, Ho TDH, Wu R (1996) Expression of a late embryogenesis abundant protein gene, HVA1, from barley conferred tolerance to water deficit and salt stress in transgenic rice. Plant Physiol. 110: 249-257.

Yamaguchi Shinozaki K, Shinozaki K (1993) Characterization of the expression of a desiccation responsive rd29 gene of *Arabidopsis thaliana* and analysis of its promoter in transgenic plants. Mol Genet Genomics. 236: 331–340.

Yamaguchi T, Blumwald E (2005) Developing salt tolerant crop plants: challenges and opportunities. Trends Plant Sci. 10: 615–620.

Yan L, Pei L, Zhao Shi X, Rui Yue Z, Li L, Lian Cheng L, Ming C, Xing Guo Y, Yao Feng C, You Zhi M (2008) Overexpression of W6 Gene Increases Salt Tolerance in Transgenic Tobacco Plants. Acta Agron Sinica. 34 (6): 984–990.

Yue Y, Zhang M, Zhang J, Duan L, Li Z (2012) SOS1 gene overexpression increased salt tolerance in transgenic tobacco by maintaining a higher K+/Na+ ratio. J Plant Physiol. 169: 255– 261.

Zhang J, Davies WJ (1989) Sequential responses of whole plant water relations towards prolonged soil drying and the mediation by xylem sap ABA concentrations in the regulation of stomatal behaviour of sunflower plants. New Phytol. 113: 167–174.

Zhang HX, Blumwald E (2001) Transgenic salt tolerant tomato plants accumulate salt in foliage but not in fruit. Nat Biotech. 19: 765-768.

Zhang HX, Hodson JN, Williams JP, Blumwald E (2001) Engineering salt tolerant Brassica plants: Characterization of yield and seed oil quality in transgenic plants with increased vacuolar sodium accumulation. P Natl Acad Sci. 98: 12832-12836.

Zhang J, Jia W, Yang J, Ismail AM (2006) Role of ABA in integrating plant responses to drought and salt stresses. Field Crops Res. 97: 111–119.

Zhu JK (2001) Plant salt tolerance. Trends Plant Sci. 6 (2).

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu rev plant biol. 53: 247-273.

Zhu JK (2003) Regulation of ion homeostasis under salt stress. Curr Opin Plant Biol. 6:441–445.

Zhu JK (2007) Plant Salt Stress: John Wiley and Sons, Ltd.