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MECHANISM OF SALINITY STRESS TOLERANCE IN CROP PLANTS AND RECENT DEVELOPMENTS

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INTRODUCTION

The last three decades has witnessed substantial increase in productivity of cereals, pulses, oilseeds and cash crops through adoption of high yielding varieties and intensive agriculture. There has been a shift from cereals to cash crops with development of high yielding varieties and increase in irrigated acreage.

Salts are component of soil, and originate from mineral weathering, inorganic fertilizers, soil amendments (e.g., gypsum, composts and manures), and irrigation waters. But when salts are present in relatively high amounts, plant growth is adversely affected. Soil salinity is a measure of the total amount of soluble salt in soil. As salinity levels increase, plants extract water less easily from soil, aggravating water stress conditions. High soil salinity afflicts about 95 million hectares of land worldwide (Szabolcs, 1994) can also cause nutrient imbalances, result in the accumulation of elements toxic to plants, and reduce water infiltration. In India, soil salinity, spread in almost 8.5 m ha area is the factor limiting plant growth and productivity.

There are two types of salinity, dry land and irrigation salinity. The dry land salinity is classified as either primary or secondary. Primary salting occurs naturally while secondary salting is induced by human

activities such as agriculture. Secondary salinity is an insidious problem that may be undetected for years until saline discharge is discovered at the soil surface. Salinity through irrigation resembles dry land salinity, except that groundwater accession is induced through irrigation water rather than rainfall alone. Irrigation salinity refers to an accumulation of salt in the plant root zone or on the soil surface, commonly as a result of saline groundwater rising within two meters of the ground surface. Classification of salt affected soil as per ICAR (ICAR 2011) are given in Table 1 and the extant of area of salt affected soil in India as identified by CSSRI, Karnal are given in Table 2.

Table 1. Classification of salt affected soil (source: Handbook of Agriculture, ICAR, 2011)

Nature of Soil	USDA Classification			SSSA Classification	
	ECe (dS m^{-1})	pH	ESP	ECe (dS m^{-1})	SAR
Normal	< 4.0	< 8.5	< 15	< 2	< 13
Saline	> 4.0	< 8.5	< 15	> 2	< 13
Sodic	Variable	> 8.5	> 15	Variable	> 13
Saline-Sodic	> 4.0	> 8.5	Variable	< 2	> 13

Table 2. Extent and distribution of salt affected soil in India (source: CSSRI, Karnal)

State	Salt affected area (× 1000 Ha)			
	Canal Command	Outside Canal	Coastal	Total
Andhra Pradesh	139	391	283	813
Bihar	224	176	Nil	400
Gujarat	540	327	302	1169
Haryana	455	Nil	Nil	455
Karnataka	51	267	86	404
Kerala	NA	NA	26	26
Madhya Pradesh	220	22	Nil	242
Maharashtra & Goa	446	NA	88	534
Odisha	NA	NA	400	400
Punjab	393	127	Nil	520
Rajasthan	138	984	Nil	1122
Tamil Nadu	257	NA	84	341
Uttar Pradesh	606	689	Nil	1295
West Bengal	Nil	NA	800	800
Total	3469	2983	2069	8521

Soil salinity negatively affects the growth of many crop plants, and the continued salinization of arable land provides an increasing threat to global crop production, especially in irrigated systems (Munns and Tester, 2008). The soil degradation mainly salinity has resulted in 4.0-6.3% crop loss in India (Table 3). Thus, understanding the mechanism and

increasing the salinity tolerance of crop plants will provide an important contribution to the maintenance of crop yields. The Na^+ toxicity of many crops is due to over accumulation of Na^+ in the shoot (Munns, 1993, 2002; Tester and Davenport, 2003; Møller and Tester, 2007). Na^+ is taken up from the soil by the root and transported to the shoot in the transpiration stream and shoot Na^+ accumulation is the net result of distinct Na^+ transport processes occurring in different organs and cell types (Tester and Davenport, 2003), and each of these processes contributes to the salinity tolerance of a plant.

Table 3. Impact of soil degradation on Indian Agriculture (Source: The cost of inaction: Valuing the economy-wide cost of environmental degradation in India, World Bank)

Crop	Percent loss
Paddy	2.7 – 4.7%
Wheat	3.9 – 6.4%
Barley	4.5 – 7.0%
Groundnut	2.8 – 4.4%
Gram	5.6 – 7.8%
Rapeseed & mustard	5.8 – 8.5%
Jowar	5.7 – 7.6%
Bajra	6.8 – 8.4%
Cotton	5.3 – 6.9%
Maize	3.2 – 4.9%
Sugarcane	4.5 – 7.9%
All other crops	4.0 – 6.3%
Total	4.0 – 6.3%

The knowledge of physiological and biochemical mechanism of salinity stress tolerance in crop plants is very important as understanding the basic responses of crop plants will help in identifying certain physiological, biochemical and molecular traits for screening of better genotypes tolerant against soil salinity which will help to identify genotypes suitable for cultivation in salt affected areas directly or through conventional breeding and biotechnological means. In this chapter an attempt was made to combine the existing knowledge of salinity tolerance in plants and the future prospect of research in this area.

2. BASIC RESPONSES OF PLANTS TO SALINITY STRESS

High salinity adversely affects germination, growth, physiology and productivity by causing ionic and osmotic stresses and oxidative damage (Iterbe-Ormaetxe *et al.*, 1998). Salt stress is also responsible for an increased respiration rate, ion toxicity (Sudhir and Murthy, 2004), changes in C and N metabolism (Kim *et al.*, 2004), mineral distribution, membrane instability (Marschner, 1986) and permeability (Gupta *et al.*,

2002), decreased biosynthesis of chlorophyll (Khan, 2003) and photosynthetic inefficiency (Munns, 2002), all of which ultimately leads to lowered economic productivity.

Accumulation of sugars and other compatible solutes that can serve as osmoprotectants, stabilizing biomolecules under stress conditions is a common phenomenon. Although use of ions for osmotic adjustment may be energetically more favorable, many plants accumulate organic osmolytes to tolerate osmotic stresses which include proline, betaine, polyols, sugar alcohols, and soluble sugars. Glycine betaine and trehalose act as osmoprotectants by stabilizing quaternary structures of proteins and highly ordered states of membranes. Proline serves as a sink for carbon and nitrogen and a free-radical scavenger, stabilizes sub cellular structures (membranes and proteins) and buffers cellular redox potential. A schematic diagram of the response of plant to salinity stress and possible changes and symptoms are given in Fig. 1.

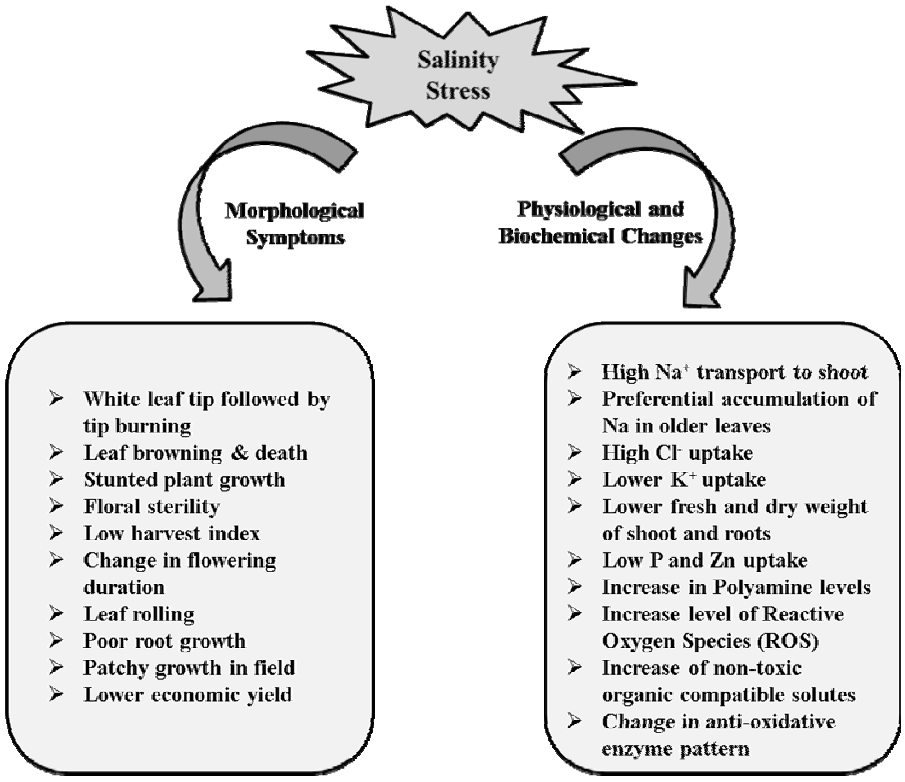

Fig. 1. Effect of soil salinity in crop plants

Salt-stress induces accumulation of reactive oxygen species (ROS), causing oxidative damage to membrane lipids, proteins, and nucleic acids. To combat oxidative stresses plants employ two strategies: i) antioxidants

(e.g., ascorbate, glutathione, α-tocopherol, and carotenoids) and ii) detoxifying enzymes, viz., superoxide dismutase, catalase, and enzymes of ascorbate-glutathione cycle. The activity and expression levels of the genes encoding detoxifying enzymes are probably enhanced by ROS under abiotic stresses.

Salt stress has both osmotic (cell dehydration) and toxic (ion accumulation) effects on whole plant and leaf physiology (Flowers, 2004). Salinity reduces the supply of CO_2 to leaves, and further depresses the already low CO_2/O_2 in chloroplasts (Remorini *et al.*, 2009). The consequent accumulation of photoreducing power causes an excess of electrochemical energy in membranes (Zhu, 2001). This extra energy is canalized through the Mehler reaction, which generates ROS such as superoxide anion ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) (Herna´ndez *et al.*, 2001), ultimately provoking oxidative-stress syndrome (Herna´ndez *et al.*, 2000; Baltruschat *et al.*, 2008).

Exposure to higher levels of NaCl affects plant water relations and creates ionic stress in the form of the cellular accumulation of Cl^- and in particular, Na^+ ions. Sodium ions if accumulated in the cytoplasm are toxic to living cells because of their adverse effects on K^+ nutrition, cytosolic enzyme activities, photosynthesis, and metabolism. Besides, salt stress also impacts heavily on the homeostasis of other ions such as Ca^{2+}, Mg^{2+}, and NO_3^- and therefore, requires insights into how transport and compartmentation of these nutrients is altered during salinity stress. Three mechanisms function cooperatively to prevent the accumulation of Na^+ in the cytoplasm, i.e., restriction of Na^+ influx, active Na^+ efflux, and compartmentalization of Na^+ in the vacuole.

Regulation of cellular ion homeostasis during salinity stress is critical for plant salt tolerance. The identification of the salt overly sensitive (SOS) pathway in *Arabidopsis* has revealed components and mechanisms involved in the plant's response to ionic stress. The DNA sequence differences of the component genes and promoters may be responsible for the variation in sensitivity of different species of *Brassica* to salt stress, as among different species of *Brassica; B. juncea* was found to be most tolerant towards salinity in terms of morphological and yield attributes followed by *B. napus* (Islam *et al.*, 2001).

3. MAJOR SYMPTOMS OF SALINITY STRESS ON CROP PLANTS

3.1. Effect of Salt Stress on Growth, Yield and Nutrient Contents

Salinity affects crop production and agricultural sustainability in many regions of the world mainly by reducing the value and productivity of the affected land (Mohammed *et al.*, 1998). Water resources in arid areas are frequently brackish and constitute the only available alternative for crop production (Botella *et al.,* 1993). Soluble salts accumulate in irrigated soils because plants absorb only a small fraction of the minerals

dissolved in irrigation water and only pure water evaporates from the soil surface, causing yield reductions (Dirksen, 1985). The species *Brassica napus* and *B. carinata* are moderately salt tolerant and have a good yield potential on the marginal lands, where as *B. juncea* and *B. compestris* are salt sensitive where reduction in stem diameter, number of siliqua per plant, 1000 seed weight and other yield attributing characters is common feature (Akhtar *et al.* 2002).

Gupta and Yadav (1986) reported that groundnut could be grown with water having EC up to 3.0 dS m^{-1}, but our recent study shows that groundnut plant starts facing salinity stress above 2.0 dS m^{-1} and EC above 4.5 dS m^{-1} kills the plants, however, as enough genotypic variation exists, the salinity level in between 3-4 dS m^{-1} during most of the cropping period was ideal for screening for salinity tolerance (Singh *et al*., 2008). In groundnut the salinity caused accumulation of Na in leaves and to compensate that and maintain proper ratio of various nutrients there was accumulation of Ca and K content. Interestingly, the salinity tolerant cultivars showed comparatively less Na and K accumulation in their leaves than that of sensitive cultivars (Singh *et al*., 2010a).

Some efforts have been made to study the performance of a few groundnut cultivars by recording germination and studying plant till vegetative phase in pots (Nautiyal *et al*., 1989; Vadez *et al*., 2005) and in field (Janila *et al*., 1999) and very few till maturity in field (Mensah *et al*., 2006; Nautiyal *et al*., 2000). Also in a recent attempt screening protocoal using rate of survival under NaCl treatment in glass house (Vadez *et al*., 2005) as well as in vitro regenerated shoots grown on media (Mungala *et al*., 2008) has been made as a measure of their tolerance to salinity. Salinity tolerance is a relative term depending mainly upon its intensity and relative performance of cultivars. The groundnut cultivars with high field emergence followed by high plant stand and low mortality under saline conditions could be considered as tolerant of salinity stress. However, data on yielding ability is more vital as increasing salinity decreases pod yield (Singh *et al*., 2008). Salinity caused severe reduction in plant stature and plant height with small immature pods followed by very high (56-100%) plant mortality at harvest (Singh *et al*., 2010a).

Assessment of the mineral nutrient status of plants facing various abiotic stresses can be done using biochemical and enzymatic methods involving marker enzymes which are based on the fact that the activity of certain enzymes in deficient tissue is lower or higher (depending on the nutrient) than in normal tissue (Lavon and Goldschmidt, 1999; Vı´llora *et al.*, 2000; Singh and Chaudhari, 1993). Catalase and peroxidase are indicators of the nutritional status of Fe in plants and are also useful as indicators of Fe and Mn deficiencies (Moreno *et al.*, 2000; Valenzuela *et al.*, 1995). Carbonic anhydrase and ribonuclease activity is a good indicator for Zn (Dwivedi and Takkar, 1974; Sharma *et al.*, 1990) and Cu deficiency increased ribonuclease activity in leaves (Agarwala *et al.*, 1985,

1995). Under salinity stress decrease in micronutrient contents are correlated with decrease in activity of related enzymes.

Salinity stress results in ionic and nutritional imbalance due to competition of salt ions with nutrients. Saline condition influences the different steps of nitrogen (N) metabolism, its uptake, reduction and protein synthesis which are responsible for the reduction in plant growth (Frechill *et al.*, 2001) and decreased dry matter production. A negative correlation between concentrations of nitrate (NO_3) and Cl^- was seen in the shoots and roots (Abdelgadir *et al.*, 2005). Salinity reduced potassium (K^+), and calcium (Ca^{2+}) contents, and increased Na^+ and Cl^- content in leaves and stems (El-Hendawy *et al.*, 2005). Saline environment is generally deficient in nitrogen (Amonkar and Karmarkar, 1995) as a result there is reduction in NO_3^- uptake due to high Cl^- in saline condition. Addition of N to salinity, improved the growth and yield of plant, and increased salt tolerance (Dubey and Pessarakli, 1995).

The most common salinity effect is a general stunting of plant growth. As salt concentration increases above a threshold level both the growth rate and size of most plant species progressively decrease but all the plant parts are not affected equally. Shoot growth is often suppressed more that the root growth (Meiri *et al.*, 1970). Often vegetative growth response to salinity is not so reliable guide for predicting seed or grain yield. Yield of rice (Pearson, 1959) and corn (Kaddah and Gohowail, 1964) are greatly reduced without affecting straw yield under saline condition. Growth and yield of bell pepper at different B and salinity levels and the results from the experiments and from published data for wheat, tomato and chickpea indicated an antagonistic relationship for excess B and salinity (Yermiyahu *et al.*, 2008). Thus, toxic effects on growth and yield were less severe for combined B toxicity and salinity than what would be expected if effects of the individual factors were additive. Though the mechanism of relationships between B and salinity in plants is not clear, the possible explanations are reduced uptake of B in the presence of Cl and reduced uptake of Cl in the presence of B (Yermiyahu *et al.*, 2008).

The crop tolerance to high B has been attributed to reduced uptake of B as a result of B efflux from roots. Salinity interacts with B toxicity by a combined effect on B and water uptake and B partitioning within the plant (Wimmer *et al.,* 2001). Salinity usually reduces shoot B concentrations. The whole tissue B concentration is a poor indicator of B tolerance, but the tissue B distribution and subcellular ion compartmentation and B and salinity interactions is important criteria in wheat (Wimmer *et al.,* 2001). Under saline conditions, the total B concentration increased in leaf tips, decreased in roots and was not affected in basal leaf parts, however, soluble B concentrations in basal leaf parts increased in the combined salt/high B treatment compared to high B treatment alone in wheat (Wimmer *et al.,* 2001). Looking to the complex relations between salinity and B toxicity the interactions of soluble B with salinity was studied on physiological response of plants in tomato plants and several

hypotheses are established by (Bastías *et al*., 2010). The increase of aquaporin functionality due to the presence of B and Ca compared with NaCl-treated plants could be the most feasible, whereas there is currently no satisfactory explanation for the results for the cell wall amino acid composition. In addition, the elemental composition results revealed that, in addition the known interactions between B and Ca with respect to cell wall stability, Mg and Mn were also increased in NaCl+B and NaCl+Ca treatments, suggesting their possible involvement in the cell wall function necessary for plant growth (Bastías *et al*., 2010).

3.2 Effect of Salinity on Pigment System of the Plant

Photosynthesis is the most important process affected in plants under saline conditions. Reduced photosynthesis under salinity is attributed to stomata closure leading to a reduction of intercellular CO_2 concentration and to non-stomatal factors also. There is strong evidence of salinity affecting photosynthetic enzymes, chlorophyll and carotenoid (Stepien and Klobus, 2006). Decrease in Chlorophyll and carotenoid contents of leaves in response to salt stress is a general phenomenon (Parida and Das, 2005). However, an increase in pigment content in *Amaranthus* sp has also been observed (Wang and Nil, 2000). The literature showed wide variations in pigment content depending on salt stress. In quite a few cases, the chlorophyll content was paralleled by changes in the Chl a/b ratio, which is an indicator of the antenna size of PS I and PS II. The core antenna contains only Chl a, whereas the outer antenna contains both Chl a and Chl b. A higher Chl a/b ratio therefore indicates a smaller antenna size and a lower ratio a larger antenna size. Chlorophyll a, b, total chlorophyll and carotenoid content decrease in response to salinity stress (Ahmad, 2009). Salt stress directly or indirectly affects the photosynthetic functions by changing the structural organization and physio-chemical properties of thylakoid membranes (Alia-Mohanti and Saradhi, 1992). Salinity stress reduces quantum yield and Fv/Fm ratio in naked oat (Zhao *et al*., 2007).

3.3. Relative Water Content and Water Availability

Salinity and water stress have quite similar effects on the growth and cell viability (Lutts *et al*., 2004). Salinity causes pronounced decrease in water uptake and plant growth in shoot and root (Misra and Dwivedi, 2004). High concentration of salt in the root zone (rhizosphere) reduces soil water potential and the availability of water (Llyod *et al*., 1989), as a result reduction of the water content dehydration at cellular level and osmotic stress are obvious. The increased amount of Na^+ and Cl^- in the soil-water medium affects the uptake of many indispensable nutrients through competitive interactions and by affecting the ion selectivity of membranes.

Salt stress reduces both RWC and fresh weight in *Brassica* genotypes, but with varied degree of reduction depending upon genotypes

(Siddiqui *et al.*, 2008). The ability of plants to utilize water as well as changes in plant metabolic processes was reduced due to salinity in bean (Munns, 2002). Water potential (Ψ) decreased considerably in the 100 mM sodium chloride and sodium sulphate-treated plants due to salinity induced cellular water loss in *Phaseolus vugaris* (Kaymakanova and Steova, 2008). The decrease in the fresh weight of plants after both salinity and drought-induced water stress have been reported for many species as one of the physiological symptoms of stress (Passioura and Munns, 2000; Sucre and Sua´rez, 2011).

3.4 Electrolyte Leakage and Membrane Stability

Cell-membrane stability, an indicator of the structural integrity, is affected by dehydration and salt stresses (Thomas, 1997). Under saline conditions, plasma-membrane leakage (an indicator of cell plasma-membrane integrity) increases and there is a linear relationship between external salinity and membrane-leakage rate (Orcutt and Nielsen, 2000). Cell-membrane stability using leaf discs in maize, subjected to osmotic stress, showed correlation with the salinity and drought resistance of the plant (Simond and Orcutt, 1988).

Increase in electrolyte leakage in the leaves of *B. juncea* with increasing levels of salinity has been reported by Ahmad *et al.* (2009). High salt depositions in the soil generate a low water potential zone making it increasingly difficult for the plant to acquire both water as well as nutrients (Mahajan and Tuteja, 2005). Thus, salt stress essentially results in a water deficit condition in the plant and takes the form of a physiological drought. Salt stress causes disruption of ionic equilibrium, influx of Na^+, dissipates the membrane potential and facilitates the uptake of Cl^- down the chemical gradient, which is evident from the reduction of membrane stability of salt treated plants. High concentration of Na^+ causes osmotic imbalance, membrane disorganization, , inhibition of cell division and expansion leading to reduction in growth. High Na^+ levels also lead to reduction in photosynthesis and production of reactive oxygen species (Yeo *et al.*, 1998).

3.5 Polyamine Biosynthesis

Polyamines (PAs) are organic poly-cations of a specific group of cell growth and development regulators and are preferentially detected in actively growing tissues and under stress conditions. Plant PA metabolism is extremely sensitive to adverse environmental conditions and hence, PAs are considered as stress markers in plants (Liu *et al.*, 2007; Takahashi and Kakehi, 2010). The function of PAs is presumed to be protective, as they act as free radical scavengers, stabilize cellular membranes, and maintain cellular balance (Bors *et al.*, 1989; Besford *et al.*, 1993). However, the precise role and mode of action of PAs in plant stress have long been a matter of debate. Changes in the levels of PAs under stress cannot be

predicted and may be affected by several factors, such as plant species or cultivar, duration of stress treatment, developmental stage of tissues, and stress intensity. In addition, cultivars of the same species but differing in stress sensitivity might also show different changes in the pattern of PAs under stress. In nine rice cultivars that differed in salt sensitivity, salt-tolerant cultivars accumulated high concentrations of Spd and Spm, while the salt-sensitive ones accumulated extensive Put and lower levels of Spd and Spm (Krishnamurthy and Bhagwat, 1989). Stress-tolerant plants generally have a large capacity to enhance PA biosynthesis in response to abiotic stresses, compared with intolerant plants (Kusano *et al*., 2008; Gill and Tuteja, 2010). In *Lupinus luteus* (a drought tolerant species), Put and Spd were accumulated in leaves in osmotic and salt-stress conditions (Legocka and Kluk, 2005). Zapata *et al*. (2004) studied the effect of salinity on plant growth, ethylene production, and PA level in *Spinacia oleracea*, *Lactuca sativa*, *Cucumis melo*, *Capsicum annum*, *Brassica oleracea*, *Beta vulgaris*, and *Lycopersicon esculentum* (Legocka and Nowicka, 2012).

4. MECHANISM OF SALINITY STRESS TOLERANCE IN CROP PLANTS

4.1 Oxidative Stress and Antioxidant Enzyme Activities

Salt stress leads to stomatal closure, reducing CO_2 availability in the leaves and carbon fixation, exposing chloroplasts to excessive excitation energy, which in turn increases the generation of reactive oxygen species (ROSs) and induce oxidative stress (Parida and Das, 2005; Parvaiz and Satyawati 2008). These ROS have potential to interact with many cellular components, causing damage to membranes and other cellular structures. However, an elaborate and highly efficient network, composed of antioxidant enzymes and antioxidants, is responsible for maintaining the levels of ROS under tight control (Gao *et al.*, 2008).

Salt induced osmotic stress as well as sodium toxicity triggers the formation of reactive oxygen species (ROS) such as superoxide ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($^{\cdot}OH$), and singlet oxygen ($^1O_2$), all of these disrups cellular structures by damaging mitochondria and chloroplasts (Mittler, 2002). Plants have developed a series of enzymatic and non-enzymatic detoxification systems to counteract ROS, and protect cells from oxidative damage (Sairam and Tyagi, 2004). The Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX) and glutathione reductase (GR) function in detoxification of super oxide and H_2O_2 (Mittler, 2002; Kholova *et al.*, 2009).

An antioxidant enzyme dependent salinity tolerance mechanism in plants is proposed in Figure 2. The SOD constitutes the primary step of cellular defence it dismutates $O_2^{\cdot-}$ to H_2O_2 and O_2. Further, the accumulation of H_2O_2 is restricted through the action of catalase or by the ascorbate glutathione cycle, where ascorbate peroxidase reduces it to H_2O.

Finally, glutathione reductase catalyzes the NADPH dependent reduction of oxidized glutathione (GSSG) to the reduced glutathione (GSH) (Noctor *et al.*, 2002). The tolerant and susceptible wheat genotypes show differences in antioxidant activity in response to salinity stress (Sairam *et al.*, 2005). Protective roles of the antioxidant enzymes in temperature and salt stress have been reported for a number of plants species (Jaleel *et al.*, 2007). The antioxidants ascorbate and glutathione are involved in scavenging H_2O_2 in conjunction with MDAR and GR, which regenerate ascorbate (Horemans *et al.*, 2000).

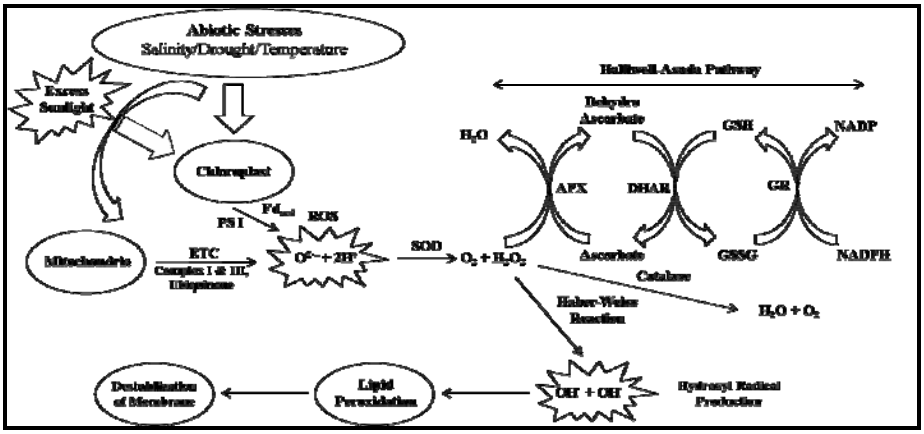

Fig. 2. Antioxidant enzyme dependent salinity tolerance mechanism in plants (modified from Mittler, 2002)

4.2 Osmotic adjustment and differential accumulation of various osmolytes

High salinity causes hyperosmotic stress and ion disequilibrium causing secondary effects (Hasegawa *et al.*, 2000; Zhu, 2001). Plants cope by either avoiding or tolerating salt stress and are either dormant during the salt episode or there is a cellular adjust to tolerate the saline environment. Tolerance mechanisms can be categorized as those that function to minimize osmotic stress or ion disequilibrium or alleviate the consequent secondary effects caused by these stresses. The chemical potential of the saline solution initially establishes a water potential imbalance between the apoplast and symplast that leads to turgor decrease, which, if severe enough, can cause growth reduction (Bohnert *et al.*, 1995). Growth cessation occurs when turgor is reduced below the yield threshold of the cell wall. Cellular dehydration begins when the water potential difference is greater than that can be compensated for by turgor loss (Taiz and Zeiger, 1998).

The cellular response to turgor reduction is osmotic adjustment which is achieved in sub-cellular compartments by accumulation of compatible osmolytes and osmoprotectants (Bohnert *et al.*, 1995; Bohnert and Jensen,

1996). However, Na^+ and Cl^- are energetically efficient osmolytes for osmotic adjustment and are compartmentalized into the vacuole to minimize cytotoxicity (Blumwald *et al.,* 2000; Niu *et al.*, 1995). Since plant cell growth occurs primarily because of directional expansion mediated by an increase in vacuolar volume, compartmentalization of Na^+ and Cl^- facilitates osmotic adjustment that is essential for cellular development. Filek *et al.* (2012) reported that Na^+ may directly or indirectly exert a positive influence on the accumulation of other compounds involved in osmotic adaptation. Such an assumption could explain the greater tolerance to osmotic stress applied in wheat seedlings grown on media containing NaCl.

Salt tolerance mechanism requires osmolytes/compatible solutes accumulation in the cytosol and organelles, where these function as osmotic adjustment and osmoprotection (Rhodes and Hanson, 1993). Some compatible osmolytes are essential ions, such as K^+, but the majority are organic solutes. Compatible solute accumulation as a response to osmotic stress is a ubiquitous process in organisms as diverse as bacteria to plants and animals. However, the solutes that accumulate vary with the organism and even between plant and genotypes. A major category of organic osmotic solutes consists of simple sugars (mainly fructose, glucose and sucrose), sugar alcohols (glycerol and methylated inositols) and complex sugars (trehalose, raffinose and fructans) (Bohnert and Jensen, 1996). Others are quaternary amino acid derivatives (proline, glycine betaine, ß-alanine betaine, proline betaine), tertiary amines 1,4,5,6-tetrahydro-2-mehyl-4-carboxyl pyrimidine), and sulfonium compounds (choline sulphate, dimethyl sulfonium propironate) (Nuccio *et al.*, 1999). Many organic osmolytes presumed to be osmoprotectants, as their level of accumulation is insufficient to facilitate osmotic adjustment. Glycine betaine preserves thylakoid and plasma membrane integrity after exposure to saline solutions or to freezing or high temperatures (Rhodes and Hanson, 1993). Many of the osmoprotectants enhance stress tolerance of plants when expressed as transgene products (Bohnert and Jensen, 1996; Zhu, 2001). An adaptive biochemical function of osmo-protectants is the scavenging of ROS that are by products of hyperosmotic and ionic stresses, causing membrane dysfunction and cell death (Bohnert and Jensen, 1996).

The accumulation of proline has been observed due to salinity in several crop species in India. Salt stress stimulated the accumulation of glycine betaine (GB) and increase in levels of malondialdehyde (MDA) content in *Brassica juncea* (Ahmad, 2009). There was an abrupt rise in osmolytes accumulation in wheat cultivars under sailinity treatment (Sairam *et al*., 2002). Tolerant genotypes of *Brassica* (CS 52 and CS 54) have inbuilt mechanism in the form of greater gene expression and activity of P5CS (pyrrolline-5-carboxylate synthetase), whose product proline provides osmotolerance in the form of retention of moisture (higher

RWC) and MSI, resulting in more yield stability (Chakraborty *et al.*, 2012b).

In plant kingdom the organisms ranging from bacteria to higher plants show a strong correlation between increased cellular proline levels and the capacity to survive both water deficit and salinity. The organic nitrogen may serve as the reserve that can be utilized during recovery from salinity. In *Lathyrus sativus*, a hardy grain legume, which can withstand drought, showed high proline accumulation in leaves and roots under water stress (Tyagi *et al.*, 1999). Though proline is synthesized either from glutamate or from ornithine, glutamate is the primary precursor in osmotically stressed cells. The biosynthetic pathway of proline accumulation consists of two important enzymes, viz. pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase and transcripts corresponding to both cDNAs accumulate in response to NaCl treatment. Both these regulatory steps are keys in developing strategies for overproducing proline in selected plant species.

4.3 Expression of Osmolarity Related Genes

A common feature of compatible solutes is that these compounds can accumulate to high levels without disturbing intracellular biochemistry and have the capacity to persevere the activity of enzymes of plants growing in saline environment (Bohnert and Jensen, 1996). These compounds have minimal effect on pH or charge balance of the cytosol or luminal compartments of organelles. The synthesis of compatible osmolytes is often achieved by diversion of basic intermediary metabolites into unique biochemical reactions. Often, stress triggers this metabolic diversion. Higher plants synthesize glycine betaine from choline by two reactions that are catalyzed in sequence by choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH). Under salt stress expression of BADH increases (Rhodes and Hanson, 1993). Pinitol is synthesized from myo-inositol by the sequential catalysis of inositol-O-methyltransferase and ononitol epimerase (Bohnert and Jensen, 1996).

Glycine betaine accumulates in many species of the poaceae and chenopodiaceae (Flowers *et al.*, 2004) but is absent in many crop species such as rice and the model species in plant transformation, *Nicotiana tabacum*. Thus considerable work on engineering the production of glycine betaine in species that do not produce it naturally is in progress. The *E. coli* has a cluster of bet genes (betA: choline dehydrogenase, betB: betaine aldehyde dehydrogenase, bet1: a putative regulatory protein and betT: the choline transport system). Transformation of a cyanobacterium with the bet cluster resulted in glycine betaine synthesis (Nomura *et al.*, 1995).

In higher plants the pathway of glycine betaine synthesis is short and straight forward. In spinach choline monooxygenase (CMO) converts choline to betaine aldehyde and betaine aldehyde dehydrogenase (BADH) converts it to glycine betaine (Burnet *et al.*, 1995). The CMO is an iron-

sulphur protein which in its native form is a homodimer (Burnet *et al.*, 1995). In sugarbeet the BADH activity increased 2 to 4-fold in leaves and roots with increase of NaCl from 0 to 500 mM and this increase in BADH activity is correlated with the level of translatable BADH mRNA. Two copies of BADH are reported in the haploid sugar beet genome and analysis of cDNA clones showed small nucleotide sequence differences consistent with the existence of two different BADH alleles (McCue and Hanson, 1992). Many species including tobacco lack both CMO and BADH. Spinach and sugarbeet cDNA sequences encoding BADH were expressed in tobacco, and even without a typical transit peptide BADH was still targeted to the chloroplast in the leaves of transgenic plants. Expressed levels and substrate affinity was comparable with the native enzyme and transgenic plants were able to synthesize glycine betaine from supplied betaine aldehyde showing a constitutive ability to transport betaine aldehyde into the chloroplast. The glycine betaine so synthesized was not metabolized further and accumulated to concentrations similar to those plants that accumulate it naturally. There is no information yet on its sub-cellular localization in transgenic plants. Betaine aldehyde is toxic when supplied exogenously in tobacco unless it was transgenic (Rathinasabapathi *et al.*, 1994). Accumulation of BADH transcripts was a common response to osmotic stress. There was 8-fold increase in BADH mRNA levels in leaves of barley under high-salt conditions, and these levels were maintained under sustained stress, but decreased when stress was removed (Ishitani *et al.*, 1995).

There are several other osmolytes than glycine betaine and one of them is trehalose, which play more than one role (Rhodes and Hanson, 1993; Yancey, 1994). TPS1 from *Saccharomyces cerevisiae* encodes trehalose–6-phosphate synthase, which is regarded as both a metabolic enzyme and a regulator (Serrano *et al.*, 1999). TPS1 has been reported to modulate the heat-shock response as well (Hazell *et al.*, 1995). Serrano *et al.* (1999) suggested that the products encoded by TPS1 may have a generalized role in activating stress-defence systems. Tobacco, transgenic for trehalose synthesis, was reported to have improved drought and salt tolerance (Romero *et al.*, 1997), but there was also a changed carbohydrate profile suggesting changes in basic biochemical pathways and the resultant average tissue concentration of trehalose (<0.5 mM) appeared too low to be performing a conventional osmoprotectant role. The transgenic plants for trehalose biosynthesis also showed linked severe morphological alterations including stunted growth.

Proline is another important metabolite which increases under salinity stress. The intermediates of proline biosynthesis and catabolism, such as glutamine and Δ-1-pyrroline-5-carboxylic acid could increase the expression of several osmotically regulated genes in rice (Iyer and Caplan, 1998). There is also evidence that degradation of proline in the mitochondria is directly coupled to respiratory electron transport system and ATP production. A pyrroline-5-carboxylate synthetase (P5CS) cDNA

from moth-bean was introduced into rice, where expression of this P5CS transgene under the control of a stress inducible promoter led to stress-induced over-production of the P5CS enzyme and proline accumulation in transgenic rice plants. Second generation (RI) transgenic plants showed an increase in biomass under salt and water stress conditions (Zhu, 1998).

4.4 Relative Distribution of K, Ca and Na in Different Plant Parts and Na Exclusion

The fundamental basis of the adaptation of plants to salinity stress is the control of transport of salt across membranes (Hasegawa *et al.*, 2000). In glycophytes, salt exclusion is the predominant strategy of adaptation to saline substrates, i.e., tolerance to salinity depends mainly on the ability of roots to limit transport of sodium (Na^+) to the leaves and shoot (Yahya, 1998). In sorghum (*Sorghum bicolor*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare* L.) and corn (*Zea mays*) which are glycophytic in nature and where (Alberico and Cramer, 1993) Na^+ exclusion mechanism is present for salt tolerance.

Also, within the plant, salt are restricted from reaching sensitive organs (Watson *et al.*, 2001). Internal exclusion mechanisms can involve processes such as sequestering salt ions in specialized tissues by removing them from the transport stream (Blom-Zandstra *et al.*, 1998; Jeschke, 1981) and/or by effectively compartmentalizing Na within vacuoles in the stem and leaf (Leigh and Storey, 1993). In other word, if Na^+ ions are not strongly discriminated against at the root membrane, salinity of the xylem stream will increase under saline conditions. Some of the ions in the transpiration stream could be selectively accumulated by parenchyma cells in the xylem and then retranslocated back to the root via phloem (Orcutt and Nielsen, 2000). The K^+ content and K^+-Na^+ selectivity decreased and electrolyte leakage was increased in different cultivars of *Brassica napus* under salt stress. Sodium import, transport and deposition were increased by salinity stress but remobilization was decreased. The K^+ and Mg^{2+} import, deposition, and remobilization were also decreased (Rezaei *et al.*, 2006).

Under saline condition salt tolerance is usually related to ability to regulate Na^+ and Cl^- uptake by plant root and their subsequent translocation to the shoot. In contrast, the higher concentration of essential elements (particularly K^+ and Ca^{2+}) in leaf tissues may contribute to the salt tolerance ability of plants (Ashraf and McNeilly, 1990; He and Cramer, 1993). The mechanism of selectivity of ion transport appears to confer tolerance to salt stress in Indian mustard. Higher selectivity towards K^+ and restricted uptake of Na^+ was observed in tolerant genotypes of Indian mustard (Kumar, 1984; Garg *et al.*, 1997).

4.5 Expression of Salt Overly Sensitive (SOS) Pathway Genes

Zhu and his co-workers identified three genetically linked *Arabidopsis* loci (*SOS1, SOS2* and *SOS3*), which are components of a

stress signalling pathway that control ion homeostasis and salt tolerance (Hasegawa *et al*,. 2000; Sanders, 2000; Zhu, 2001). Genetic analysis of Na^+/Li^+ sensitivity established that *sos1* is epistatic to *sos2* and *sos3*. These *sos* mutants also exhibit a K^+ deficient phenotype in medium supplemented with µM $[K^+]_{ext}$ and $[Ca^{2+}]_{ext}$. Na^+ and K^+ deficiency of *sos2* and *sos3* is suppressed with mM $[Ca^{2+}]_{ext}$ (Zhu *et al.,* 1998). The *sos1* exhibits hyperosmotic sensitivity unlike *sos3* and *sos2*. Thus, the SOS signaling pathway regulates Na^+ and K^+ homeostasis and is Ca^{2+} activated. SOS3 encodes a Ca^{2+} binding protein with sequence similarity to the regulatory B subunit of calcineurin (protein phosphatase 2B) and neuronal Ca^{2+} sensors (Ishitani *et al.,* 2000; Liu and Zhu, 1998). Interaction of SOS3 with the SOS2 kinase (Liu *et al.*, 2000) and SOS2 activation is Ca^{2+} dependent (Halfter *et al.,* 2000). The *in planta* function of SOS3 as a salt tolerance determinant is dependent on Ca^{2+} binding and N-myristoylation (Ishitani *et al.*, 2000). After Zhu (*et al.*, 2001) we Propose a SOS Pathway for Na^+ homeostasis in plants as in Fig. 3.

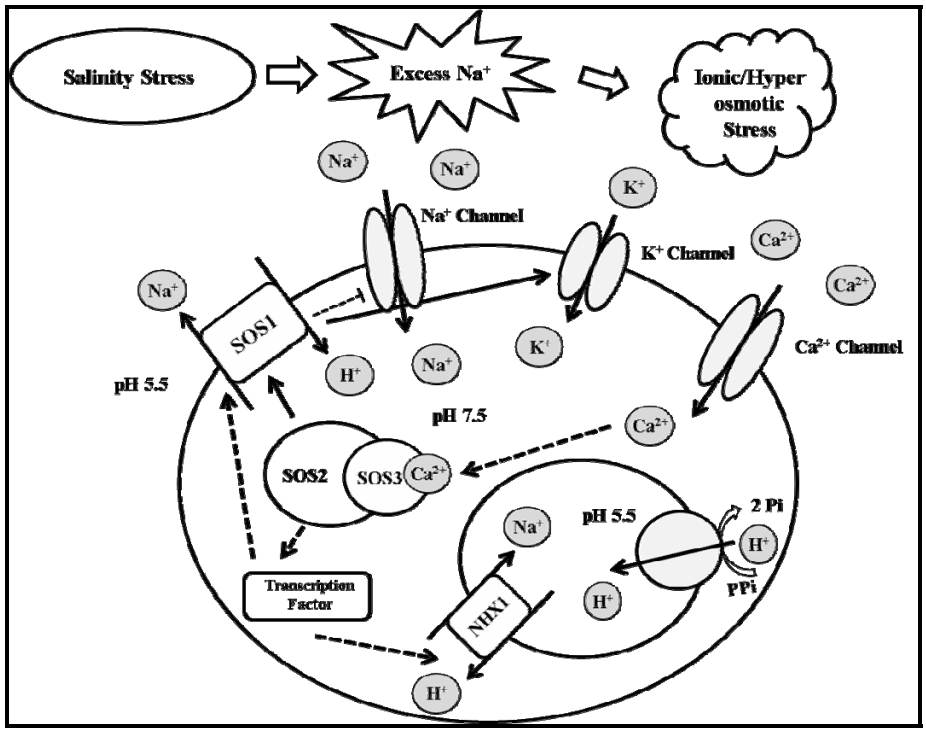

Fig. 3. Proposed Salt Overly Sensitive (SOS) Pathway for Na^+ homeostasis in plants (Modified from Zhu *et al.*, 2001)

The SOS2 serine/threonine kinase (446 amino acids) has a 267 amino acid N-terminal catalytic domain that is similar in sequence to yeast SNF1 (sucrose non-fermenting) kinase and the mammalian AMPK (AMP-activated protein kinase) (Liu *et al.,* 2000; Zhu, 2001). The kinase activity

of SOS2 is essential for its salt tolerance determinant function (Zhu, 2001). The SOS2 C-terminal regulatory domain interacts with the kinase domain to cause autoinhibition. A 21 amino acid motif in the regulatory domain of SOS2 is the site where SOS3 interacts with the kinase and is the autoinhibitory domain of the kinase (Guo *et al.*, 2001). Binding of SOS3 to this motif blocks autoinhibition of SOS2 kinase activity. Deletion of the autoinhibitory domain results in constitutive SOS2 activation, independent of SOS3. Also, a Thr_{168} to Asp mutation in the activation loop of the kinase domain constitutively activates SOS2.

Genetic and biochemical evidences indicate that components of the SOS signal pathway function in the hierarchical sequence (Hasegawa *et al.*, 2000; Sanders, 2000; Zhu, 2001). The Ca^{2+} binds to SOS3 which leads to interaction with SOS2 and activation of the kinase. Among the SOS signal pathway outputs are transport systems that facilitate ion homeostasis. The plasma membrane sited Na^+/H^+ antiporter SOS1 is controlled by the SOS pathway at the transcriptional and post-transcriptional level (Guo *et al.*, 2001; Zhu, 2001). Recently, functional disruption of *AtHKT1* was shown to suppress the salt sensitive phenotype of *sos3-1*, indicating that the SOS pathway negatively controls this Na^+ influx system (Rus *et al.*, 2001). Also, the SOS pathway negatively controls expression of *AtNHX* family members that are implicated as determinants in the salt stress response (Yokoi *et al.*, 2002). Chakraborty *et al.* (2012a) reported that mechanism governing salinity tolerance in *Brassica* could be the significantly higher induction of genes coding components of SOS pathway, viz., *SOS1*, *SOS2*, *SOS3* and vacuolar antiporter *NHX1*, resulting in restricted uptake of toxic Na^+ ,and efficient Na-exclusion and sequestration system, which was manifested in lesser reduction in tissue K^+ content and higher K/Na ratio under salt stress, paving the way for better ion homeostasis and salinity tolerance.

The $[Ca^{2+}]_{ext}$ enhances salt tolerance and salinity stress elicits a transient $[Ca^{2+}]_{ext}$ increase, from either an internal or external source, implicated in adaptation (Knight *et al.*, 1997, Läuchli, 1996). Experiments with yeast have provided insight into Ca^{2+} activation of salt stress signalling that controls ion homeostasis and tolerance (Matsumoto *et al.*, 2001). The hyperosmotic component of high salinity induces a short duration of about 1 minute rise in $[Ca^{2+}]_{ext}$ that is due substantially to influx across the plasma membrane through the Cch1p and Mid1p Ca^{2+} transport system. The transient increase in $[Ca^{2+}]_{ext}$ activates the PP2B phosphatase calcineurin; a key intermediate in salt stress signalling controlling ion homeostasis, leading to the transcription of *ENA1*, which encodes the P-type ATPase primarily responsible for Na^+ efflux across the plasma membrane (Nakamura *et al.*, 1993; Mendoza *et al.*, 1994; Matsumoto *et al.*, 2001). The model proposes that the hyperosmotically-induced localized $[Ca^{2+}]_{ext}$ transient activates calmodulin that is tethered to Cch1p-Midp (Ehlers and Augustine, 1999; Sanders, 2000; Matsumoto *et al.*,2001). Calmodulin in turn activates signalling through the calcineurin

pathway, which mediates ion homeostasis and salt tolerance (Matsumoto *et al.*, 2001).

Thus a paradigm for salt-induced Ca^{2+} signalling and the activation of the SOS pathway can be suggested. Components of the SOS pathway, either SOS3 or upstream elements, might be associated with an osmotically responsive channel through which Ca^{2+} influx could initiate signalling through the pathway. It is notable that a new elevated $[Ca^{2+}]_{ext}$ steady state is established in yeast cells, that are maintained in medium supplemented with NaCl, after the hyperosmotic induction of the short duration $[Ca^{2+}]_{ext}$ transient (Matsumoto *et al.*, 2001). The newly established $[Ca^{2+}]_{cyt}$ is likely to contribute to cellular capacity for growth in salinity. The vacuolar membrane H^+/Ca^{2+} antiporter Vcx1p and endomembrane localized Ca^{2+}-ATPases are pivotal effectors that regulate the amplitude and duration of the $[Ca^{2+}]_{ext}$ transient (Miseta *et al.*, 1999). The $[Ca^{2+}]_{ext}$ steady state established in salt containing medium presumably also involves coordination of channel activation that facilitates influx from external and internal sources and energy dependent transport systems that compartmentalize the divalent cation. It is reasonable to assume that the salt induced $[Ca^{2+}]_{ext}$ transient detected in plant cells (Knight, 1997) and, perhaps, a new $[Ca^{2+}]_{ext}$ steady-state are controlled by the ECA and ACA Ca^{2+}-ATPases and CAX1 and 2 transporters which are orthologs of Vcx1p (Sze *et al.*, 2000). Nevertheless, Ca^{2+} has at least two roles in salt tolerance, a pivotal signaling function in the salt stress response leading to adaptation and a direct inhibitory effect on a Na^+ entry system.

5. SALT TOLERANT CROP PLANTS

The restriction of uptake and transport and internal tolerance mechanisms are the two important criteria which plants employ to combat high external concentrations and hence tolerance could be attributed to the lower the content and lower uptake or accumulation of these in the root and shoot and high yield in toxic soils (Singh *et al.*, 2010b). Ameliorating high-mineral soils using soil amendments is expensive and extremely difficult. Use of tolerant crop genotypes, phytoremediation by tolerant crops, and inoculations of beneficial microorganisms are the solutions (Singh *et al.*, 2010b). The salt tolerance of a crop can best be described by plotting its relative yield as a continuous function of soil salinity (Fig 4). For most crops, this response function follows a sigmoidal relationship however, several crops may die before the seed or fruit yields decrease to zero, thus eliminating the bottom part of the sigmoidal curve (Maas and Hoffman, 1977). By plotting relative yield with increasing soil salinity level a threshold level of soil salinity is obtained for some of the crops which have its greatest value in providing general salt tolerance guidelines for crop management decisions. Farmers need to know the soil salinity levels that begin to reduce yield and how much yield will be reduced at levels above the threshold. However, more precise plant

response functions would be advantageous for crop simulation modelling (van Genuchten and Hoffman, 1984). From the experimental data in general the plants were classified in four categories according to their response to salinity (Bernstein, 1962).

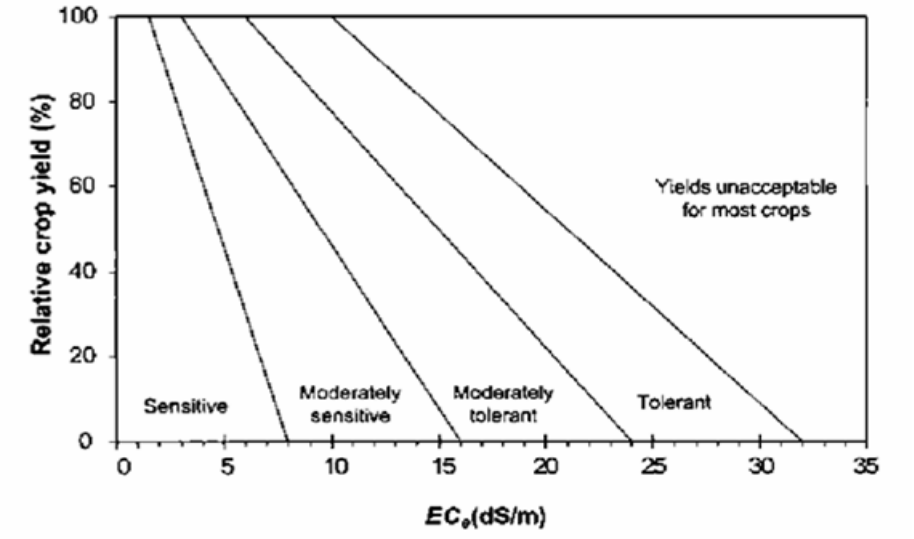

Fig. 4. Classification of the crop based on soil salinity level (source: FAO Report)

Accordingly, threshold salinity level which can cause damage, level of loss with further increase in salinity and some of the recommended crop cultivars suitable for growing in salt affected areas is listed for the important crops cultivated in India are listed in Table 4. The last column provides a qualitative salt tolerance rating that is useful in categorizing crops in general terms.

Table 4. List of field crops with their salinity tolerance level and suitable cultivars for cultivation in salt affected areas (source: FAO, ICAR, CSSRI reports)

Crop		Salinity tolerance level		Tolerant Cultivars	Over all nature of the crop*
Common Name	Botanical Name	Threshold level (dS m^{-1})	% loss per dSm^{-1} rise		
Rice	*Oryza sativa* L.	3.0	12.0	Lunishree, Sonamani, Pokkali, Nona Bokra, IR 8, Damodar, PVR 1, Basmati HBC19, Basmati 370, CSR 11, CSR 13, CSR 27, IR 28	S
Wheat	*Triticum aestivum* L.	6.0	7.1	KRL 1-4, KRL 19, Kharchia, KRL 210, KRL 213, KRL 99, KRL 35	MT

Indian Mustard	*Brassica juncea* L.	--	--	CS 52, CS 54, CS 56, Urvashi	MS
Barley	*Hordeum vulgare* L.	6.0	7.1	BH 924, RD 2508, Ratna, R 56	MT
Chick pea	*Cicer arietinum* L.	--	--	Pusa 256, Pusa 329, Pusa362, BGD 87, CSG 9651, BG 267, Karnal Chana 1, CSG 88101	MS
Soybean	*Glycine max* (L.) Merrill	5.0	20.0	CoSoy 2, DS 40, PalamSoy, Pusa 16	MT
Cotton	*Gossypium hirsutum* L.	7.7	5.2	Arya-Anubam, RAHS 14, Dhumad, Jayadhar, A 82-1	T
Sesame	*Sesamum indicum* L.	--	--	RT 54, RT 46, RT 127	S
Oat	*Avena sativa* L.	--	--	JHO 815, JHO 802, JHO 816, UPO 201	T
Groundnut	*Arachis hypogaea* L.	3.2	29.0	GG 4, MH 2, ICGV 86590, ICGS 44, Gangapuri, TG 37A, Kopergaon 3, VRI 4	MS
Sorghum	*Sorghum bicolor* (L.) Moench	6.8	16.0	JJ 1041, ICSB 707, CSV 15, S 35	MT
Sugarcane	*Saccharum officinarum* L.	1.7	5.9	Neeraj (Co 99006), Damodar (Co 99004), CoJ 20193	MS
Pigeon pea	*Cajanus cajan* (L.) Huth	--	--	H06-12, Pusa 991, JBP 110-B, ICPL 2037, ICPB 2039	S

* T: Tolerant, MT: Moderately Tolerant, S: Susceptible, MS: Moderately Susceptible

6. CONCLUSION AND FUTURE RESEARCH STRATEGIES

Soil salinity adversely affects plant growth and development accompanied by an increase in uptake of Na^+ and Cl^- ions and a decrease in uptake of K^+, Ca^{2+}, Mg^{2+} resulting in ionic imbalance, sodium ion injury and disturbed metabolic processes, changed concentration of biomolecules, photosynthetic activity and poor productivity. Although, the wild species are very much inferior in terms of yield and other agronomic characters but when it is to face the adverse environment, they show much more competence compared to cultivated agronomically superior genotypes. It is found that external application of potassium helps to maintain the K/Na ratio inside the plant tissue for smooth functioning of the cell. Sometimes, foliar application of certain plant growth regulators like salicylic acid, abscisic acid and polyamine viz. spermine, spermidine, putrescine, cadaverine etc. seems to ameliorate the adverse effect of salt stress in plants.

Tolerance capacity of the plants vastly depends up on its mechanism to overcome the salt stress through osmotic adjustment by accumulating compatible solutes inside the cell and thereby reducing the osmotic potential of the cell. This adaptation strategy helps the plants to still take

up water from rhizosphere zone, when the water potential there goes well below normal level due to soil water salinity. Other most detrimental effect faced by the plants is sudden outburst of reactive oxygen species produced due to salinity stress, which disrupts the cellular structure and damages subcellular organelles, leading to cell death. The genotypes having better antioxidant defence capacity are more capable of combating the stress.

At molecular level, efficient operation of different signal proteins and various symporters and antiportes lying either in the plasma-membrane or tonoplast play important role in salinity tolerance. Activity of different Na^+/H^+ antiporters viz. SOS1 and NHX1 depends up on the activation of other signal proteins like SOS2, SOS3 and other calcium binding proteins. Apart from these, several transcription factors like *WRKY*, *DREB*, *CBF* also contribute towards salinity tolerance in plants. The physiological, biochemical and molecular biological knowledge on salinity tolerance in crop plants are important for understanding the responses and identification of the parameters for developing screening methodologies for all crop plants.

Incredible advances have been made over the last four decades to understand the response of plants towards soil and water salinity and their management, and most of the works are focused on revealing the inherent capacity of the plants to combat the ill effect of salt stress. However, only very few works has brought finished product either in the form of genetically improved varieties through biotechnological or conventional crop improvement means or in the form of some good management practices. This need consolidated effort to come out with answer to the problem of soil salinity.

Optimistically, discussing the avenues for future research strategies following approaches may be useful towards proving salinity tolerance in crop plants.

- Development of suitable methodologies for screening for salinity tolerance in all the crops and then its subsequent recommendations in saline areas.
- Exploration of all the available natural resources needs to be carried out to manage salinity in field.
- Use of known tolerant varieties/genotypes and their further improvement for yield and tolerance level.
- Mining of the differentially expressed genes from the wild relatives of the cultivated species, and subsequent transfer of those to cultivable species either through molecular or conventional plant breeding could be a possible way.

To characterise these wild genotypes for their tolerance behaviour to single or multiple stresses and search for the candidate genes responsible for the tolerance. The major setback faced by the breeders in this approach is that most of wild tolerant genotypes are often cross-incompatible with

the cultivated species where there is a need to go for more precise method of gene transfer using biotechnological tools.

Search for novel salt tolerant genes or protein should be done not only in the related plant and crop species, rather sources of tolerance can also be explored in some known halophytic plants like mangroves and others which can thrive well under extremely saline environment, as nowadays it is possible to transfer target gene(s) from any organism to other. However, such type of work has been initiated by some of the reputed laboratories in India and abroad with a mission to successfully transfer the important genes imparting tolerance to soil salinity from mangrove gene pool to some of important crop plants like rice and others. Besides this, mining of the genes are also possible from wide range of microbial gene pool as well as that of *Archea*. Apart from the commonly known pathways that impart tolerance to eukaryotes including higher plants, there may be some other operating mechanism in these organisms which make them able to survive in the salty environment of sea or saline hot spring.

Few preliminary works suggest that by altering the promoter region of the genes it is possible to fetch tolerance towards various abiotic stresses. As these promoter elements work upstream to many of the genes involved in same or different pathways, so by up-regulating their function one can bring tolerance to susceptible genotypes. The proteins like dehydration-responsive element-binding proteins (DREBs), or C-repeat-binding proteins (CBFs), are among the first families of transcriptional regulators that are transcriptionally up-regulated by salinity, water deficit or low temperature stress. Also, the *WRKY* gene family has been suggested to play important roles in the regulation of transcriptional reprogramming associated with plant stress responses. Modification of the expression patterns of *WRKY* genes and/or changes in their activity contribute to the elaboration of various signalling pathways and regulatory networks.

The genotypes having superior antioxidant defence capacity in terms of either accumulation of antioxidants like ascorbic acid, glutathione, malonaldehyde etc. or higher activity of the enzymes viz. superoxide dismutase, ascorbate peroxidase, catalase, glutathione reductase, peroxidase etc. are more capable of withstanding salinity stress. Salinity stress cause osmotic and oxidative stress, hence genetic modifications in these areas could yield beneficial result in bringing salinity tolerance in crop plants. Incorporation of genes facilitating biosynthesis of compatible solutes whose accumulation will help in osmotic adjustment in the plant cell thereby maintaining better water balance inside the plant tissues when it is facing osmotic pressure from outside.

Though there is ample opportunity for research in this area, it needs multidisciplinary approaches to address all the component of the problem of salinity. Although, spectacular results leading to development of salt tolerant varieties capable enough to give comparable yield like agronomical superior varieties is unlikely. Integrated research programme

soil scientists, plant breeders, agronomists, physiology and molecular biologists can yield some future product to solve the salinity problem.

REFERENCES

Abdelgadir, E; Ka, MA and Fujiyama, H 2005. Nitrogen nutrition of rice plants under salinity. *Biol. Plant.,* 49: 99–104.

Agarwala, SC; Chatterjee, C; Sharma, CP and Nautiyal, N 1985. Copper nutrition of sugarbeet. *J. Exp. Bot.,* 36: 881–888.

Ahmad, P 2009. Growth and antioxidant responses in mustard (Brassica juncea L.) plants subjected to combined effect of gibberellic acid and salinity. *Achives Agron. Soil Sc.,* (i*First* Article). 1-14.

Akhtar, J; Tanveer-ul-Haq; Saqib, M and Mahmood, K 2002. Effect of salinity on yield, growth and oil contents of four *Brassica* species. *Pak. J. Agri Sci.,* 39: 76-79.

Alberico, GL and Cramer, GR 1993. Is the salt tolerance of maize related to sodium exclusion? I. Preliminary screening of seven cultivars. *J. Plant Nutri.,* 16: 1289–1303.

Alia-Mohanty, P and Saradhi, PP 1992. Effect of sodium chloride on primary photochemical activities in cotyledonary leaves of *Brassica juncea. Biochem. Physiol.*, 188: 1-12.

Amonkar, DV and Karmarkar SM 1995. Nitrogen uptake and assimilation in halophytes. In: Nitrogen nutrition in higher plants, eds. H. S. Srivastava, and R. P. Singh. New Delhi, India: Associated Publishers Company. pp. 431–445.

Ashraf, M and McNeilly, T 1990. Responses of four *Brassica* species to sodium chloride. *Environ. Exp. Bot.,* 30: 475–487.

Baltruschat, H; Fodor, J; Harrach, BD; Niemczyk, E; Barna, B and Gullner, G 2008. Salt tolerance of barley induced by the root endophyte Piriformospora indica is associated with a strong increase in antioxidants. *New Phytol.*, 180: 501–10.

Bernstein, L 1962. Salt-affected soils and plants. In: Proc. of the 18th UNESCO Symposium on Problems of the Arid Zones. Paris. pp. 139-174.

Besford, RT; Richardson, CM; Campos, JL and Tiburcio, AF 1993. Effect of polyamines on stabilization of molecular complexes in thylakoid membranes of osmotically stressed oat leaves. *Planta,* 189: 201–206.

Blom-Zandstra, M; Vogelzang, SA and Veen, BW 1998. Sodium fluxes in sweet pepper exposed to varying sodium concentrations. *J. Exp. Bot.,* 49: 1863–1868.

Blumwald, E.; Aharon, GS and Apse, MP 2000. Sodium transport in plant cells. *Biochemica et Biophysica Acta,* 1465: 140-151.

Bohnert, HJ and Jensen, RG 1996. Strategies for engineering water stress tolerance in plants. *Trends Biotech.,* 14: 89-97.

Bohnert, HJ; Nelson, DE and Jensen, RG 1995. Adaptations to environmental stresses. *Plant Cell,* 7: 1099-1111.

Bors, W; Langebartels, C; Michel, C and Sandermann, JH 1989. Polyamines as radical scavengers and protectants against ozone damage. *Phytochemistry,* 28: 1589–1595.

Botella, MA; Cerda, AC and Lips, SH 1993. Dry matter production, yield, and allocation of carbon-14 assimilates by wheat as affected by Nitrogen sources and salinity. *Agron. J.*, 85: 1044-1049.

Burnet, M; LaFontaine, PJ and Hanson, AD 1995. Assay, purification, and partial characterisation of choline monooxygenase from spinach. *Plant Physiol.* 108: 581–588.

Chakraborty, K; Sairam RK and Bhattacharya, RC 2012b. Salinity induced expression of pyrrolline-5-carboxylate synthetase determine salinity tolerance in Brassica spp. *Acta Physiol. Plant.*, 34: 1935-41.

Chakraborty, K; Sairam, RK and Bhattacharya, RC 2012a. Differential expression of salt overly sensitive pathway genes determines salinity stress tolerance in Brassica genotypes. *Plant Physiol. Biochem.,* 51: 90-101.

Dirksen, C 1985. Relationship between root uptake weighted mean soil salinity and total leaf water potentials of alfalfa. *Irrig. Sci.*, 6: 39-50.

Dubey, RS and Pessarakli, M 1995. Physiological mechanisms of nitrogen absorption and assimilation in plants under stressful conditions. In: Handbook of Plant and Crop Physiology, eds. M. Pessarakli New York: Marcel Dekker, pp. 605–625.

Dwivedi, RS and Takkar, PN 1974. Ribonuclease activity as an index of hidden hunger of Zn in crops. *Plant Soil,* 40: 173–181.

Ehlers, MD and Augustine GJ 1999. Cell signaling. Calmodulin at the channel gate. *Nature,* 399: 105-107.

El-Hendawy, SE; Hu, Y and Schmidhalter, U 2005. Growth, ion content, gas exchange, and water relations of wheat genotypes differing in salt tolerances. *Aust. J. Agril. Res.,* 56: 123–134.

Filek, M; Walas, S; Mrowiec, H; Rudolphy-Sko´rska, E; Sieprawska, A and Biesaga-Kos cielniak J 2012. Membrane permeability and micro- and macro element accumulation in spring wheat cultivars during the short-term effect of salinity- and PEG-induced water stress. *Acta Physiol Plant.,* 34**:** 985–995.

Flowers, TJ 2004. Improving crop salt tolerance. *J.Exp.Bot.,* 55: 307–319.

Frechill, S; Lassa, B; Ibarretxe, L; Lamsfus, C and Aparicio Trejo, P 2001. Pea responses to saline stress in affected by the source of nitrogen nutrition (ammonium or nitrate). *Plant Growth Regul.,* 35: 171–179.

Gao, S; Ouyang, C; Wang, S; Xu, Y; Tang, L and Chen, F 2008. Effects of salt stress on growth, antioxidant enzyme and phenylalanine ammonia lyase activities in *Jatropha curcas* L. seedlings. *Plant Soil Environ.,* 54: 374–381.

Garg, BK; Kathju, S; Vyas, SP and Lahiri, AN 1997. Genotypic difference to salt stress in Indian mustard. In: Proc. Symposium on Recent Advances in Management of Arid Ecosystems, held at Central Arid Zone Research Institute, Jodhpur, 3–5 March. Rajasthan, India: Arid Zone Research Association of India.

Gill, SS and Tuteja, N 2010. Polyamines and abiotic stress tolerance in plants. *Plant Signal Behav.,* 5: 26–33.

Guo, Y; Halfter, U; Ishitani, M and Zhu, JK 2001. Molecular characterization of functional domains in the protein kinase SOS2 that is required for plant salt tolerance. *Plant Cell,* 13: 1383-400.

Gupta, IC and Yadav, JSP 1986. Crop tolerance to saline irrigation waters. *J. Ind. Soc. Soil Sci.,* 34: 379-386.

Gupta, NK; Meena, SK; Gupta, S. and Khandelwal, SK 2002. Gas exchange, membrane permeability, and ion uptake in two Species of indian jujube differing in salt tolerance. *Photosyntetica,* 40: 535-539.

Hasegawa, PM; Bressan, RA; Zhu, JK and Bohnert, HJ 2000. Plant cellular and molecular responses to high salinity. *Ann. Rev. Plant Physiol. Plant Mol. Biol.,* 51: 463–499.

Hazell, BW; Nevalainen, H and Attfield, PV 1995. Evidence that *Saccharomyces cerevisiae* CIF1 (GGS1/TPS1) gene modulates heat shock response positively. *FEBS Letters,* 377: 457–460.

He, T and Cramer, GR 1993. Growth and ion accumulation of the two rapid-cycling *Brassica* species differing in salt tolerance. *Plant Soil,* 153: 19–31.

Hernandez, JA; Ferrer, MA; Jimenez, A; Barcelo, AR and Sevilla F 2001. Antioxidant systems and $O^{2\cdot}/H_2O_2$ production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. *Plant Physiol.,* 127: 817–831.

Hernandez, JA; Jimenez, A; Mullineaux, P and Sevilla, F 2000. Tolerance of pea (*Pisum sativum* L.) to long term salt stress is associated with induction of antioxidant defences. *Plant Cell Environ.,* 23: 853–862.

Horemans, N; Foyer CH; Potters, G and Asard, H 2000. Ascorbate function and associated transport systems in plants. *Plant Physiol. Biochem.,* 38: 531–540.

Ishitani, M; Liu, J; Halfter, U; Kim, CS; Shi, W and Zhu, JK 2000. SOS3 function in plant salt tolerance requires Nmyristoylation and calcium binding. *Plant Cell,* 12: 1667-1677.

Ishitani, M; Nakamura, T; Han, SY and Takabe, T 1995. Expression of the betaine aldehyde dehydrogenase gene in barley in response to osmotic stress and abscisic acid. *Plant Mol. Biol.,* 27: 307–315.

Islam, MR; Bhuiyan, AR; Prasad, B; Rashid, MH and Quddus, MA 2001. Salinity effect on yield and component characters in Rapeseed and Mustard varieties. *J. Biol. Sci.,* 1: 840-842.

Iterbe-Ormaetxe, I; Escuredo, PR; Arrese-Igor, C and Becana, M 1998. Oxidative damage in pea plants exposed to water deficit of paraquat. *Plant Physiol.*, 161**:** 173-181.

Iyer, S and Caplan, A 1998. Products of proline catabolism can induce osmotically regulated genes in rice. *Plant Physiol.,* 116: 203–211.

Jaleel, CA; Gopi, R; Manivannan, P and Panneerselvam, R 2007. Antioxidative potentials as a protective mechanism in *Catharanthus roseus* (L.) G.Don. plants under Salinity Stress. *Turk. J. Bot.,* 31: 245-251.

Janila, P; Rao, TN and Kumar, AA 1999. Germination and early seedling growth of groundnut (*Arachis hypogaea* L.) varieties under salt stress. *Annals Agric. Res.,* 20: 180–182.

Jeschke, WD and Nassery, H 1981. K^+-Na^+ selectivity in roots of Triticum, Helianthus and Allium. *Physiol. Plant*., 52: 217-224.

Kaddah, MT and Ghowail, SI 1964. Salinity effects on the growth of corn at different stages of development. *Agron. J.*, 64: 214-217.

Kaymakanova, M and Steova, N 2008. Effect of salt stress on growth and photosynthesis rate of bean plants (*Phaseolus vulgaris* L.). *J. Cen. Europ. Agri.,* 9**:** 385-392.

Khan, NA 2003. NaCl inhibited chlorophyll synthesis and associated changes in ethylene evolution and antioxidative enzyme activities in wheat. *Biol. Plant*., 47**:** 437-440.

Kholová J; Sairam, RK; Meena, RC and Srivastava GC 2009. Response of maize genotypes to salinity stress in relation to osmolytes and metal-ions contents, oxidative stress and antioxidant enzymes activity. *Biol. Plant*., 53: 249-256.

Kim, Y; Arihara, J; Nakayama, T; Nakayama, N; Shimada, S and Usui, K 2004. Antioxidative responses and their relation to salt tolerance in *Echinochloa oryzicola* vasing and *Steraia virdis* (L.) Beauv. *Plant Growth Regul.,* 44: 87-92.

Knight, H; Trewavas, AJ and Knight, MR 1997. Calcium signaling in *Arabidopsis thaliana* responding to drought and salinity. *Plant J.,* 12: 1067-1078.

Krishnamurthy, R and Bhagwat, KA 1989. Polyamines as modulators of salt tolerance in rice cultivars. *Plant Physiol.,* 91: 500–504.

Kumar, D 1984. The value of certain plant parameters as an index for salt tolerance in Indian mustard *(Brassica juncea L.). Plant Soil,* 79: 261–272.

Kusano, T; Berberich T; Tateda C and Takanashi Y 2008. Polyamines: essentials factors for growth and survival. *Planta,* 228: 367–381.

Lauchli, A 1996. Calcium in Plant Growth and Development, eds. Leonald, R. T. and Hepler, P. K. The American Society of Plant Physiologists Symposium Series (American Society of Plant Physiologists. Rockvill, MD) **4**: 26-35.

Lavon, R and Goldschmidt, E 1999. Enzymatic methods for detection of mineral element deficiencies in Citrus leaves: a mini-review. *J. Plant Nutr.,* 22: 139–150.

Legocka, J and Kluk, A 2005. Effect of salt and osmotic stress on changes in polyamine content and arginine decarboxylase activity in *Lupinus luteus* seedlings. *J. Plant Physiol.*, 162: 662–668.

Legocka, J and Sobieszczuk-Nowicka, E 2012. Sorbitol and NaCl stresses affect free, microsome-associated and thylakoid-associated polyamine content in *Zea mays* and *Phaseolus vulgaris. Acta Physiol. Plant.,* 34: 1145–1151.

Leigh, RA and Storey, R 1993. Intercellular compartmentation of ions in barley leaves in relation to potassium nutrition and salinity. *J. Exp. Bot.,* 44: 755–762.

Liu, J and Zhu, JK 1998. A calcium sensor homolog required for plant salt tolerance. *Science,* 280: 1943–1945.

Liu, J; Ishitani, M; Halfter, U; Kim, CS and Zhu, JK 2000. The *Arabidopsis thaliana* SOS2 gene encodes a protein kinase that is required for salt tolerance. *Proc. Natl. Acad. Sci. USA,* 97: 3730–3734.

Liu, JH; Kitashiba, H; Wang, J; Ban, Y and Moriguchi, T 2007. Polyamines and their ability to prove environmental stress tolerance to plants. *Plant Biotechnol.,* 24: 117–126.

Maas, EV and Hoffman, GJ 1977. Crop salt tolerance - current assessment. *J. Irrig. Drainage Div.*, ASCE 103 (IR2): 115-134.

Mahajan, S and Tuteja, N 2005. Cold, salinity and drought stresses. *Archives Biochem. Biophy.,* 444: 139-158.

Marschner, H 1986. Mineral nutrition in higher plants. Academic Press, London, pp. 477-542.

Matsumoto, TK; Ellsmore, AJ; Cessna, SG; Low, P; Pardo, JM; Bressan, RA and Hasegawa, PM 2001. An osmotically induced cytosolic Ca^{2+} transient activates calcineurin signaling to mediate ion homeostasis and salt tolerance of *Saccharomyces cerevisiae.*

McCue, KF and Hanson, AD 1992. Salt-inducible betaine aldehyde dehydrogenase from sugar beet—cDNA cloning and expression. *Plant Mol. Biol.,* 18**:** 1–11.

Meiri, A and Poljakoff-Mayber, A 1970. Effect of various salinity regimes on growth, Leaf expansion and Transpiration rate of Bean plants. *Soil Sci.,* 109: 26-34.

Mendoza, I; Rubio, F; Rodriguez-Navarro, A and Pardo, JM 1994. The protein phosphatase calcineurin is essential for NaCl tolerance of *Saccharomyces cerevisiae*. *J. Biol. Chem.,* 269: 8792–8796.

Mensah, JK; Akomeah, PA; Ikhajiagbe, B and Ekpekurede, EO 2006. Effect of salinity on germination, growth and yield of five groundnut genotypes. *African J. Biotech.* 5: 1973–1979.

Miseta, A; Kellermayer, R; Aiello, DP; Fu, L and Bedwell, DM 1999. The vacuolar Ca^{2+}/H^{+} exchanger Vcx1p/Hum1p tightly controls cytosolic Ca^{2+} levels in *S. cerevisiae*. *FEBS Letters,* 451: 132-136.

Misra, N and Dwivedi, UN 2004. Genotypic difference in salinity tolerance of green gram cultivars. *Plant Sci.*, 166: 1135-1142.

Mittler, R 2002. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.*, 7: 405- 410.

Mohammed, M; Shibli, R; Ajlouni, M and Nimri, L 1998. Tomato root and shoot responses to salt stress under different levels of phosphorus nutrition. *J. Plant Nutr.*, 21: 1667- 1680.

Møller, IS and Tester, M 2007. Salinity tolerance of Arabidopsis: a good model for cereals? *Trends Plant Sci.*, 12**:** 534–540.

Moreno, DA; Vıllora, G; Pulgar, G and Romero, L 2000. Effect of nitrogen and potassium supply on concentration of iron and manganese and activities of catalase, peroxidase and aconitase in pepper plants. *J. Plant Nutr.*, 23: 1787–1795.

Mungala, AJ; Radhakrishnan, T and Dobaria, JR 2008. In vitro screening of 123 Indian peanut cultivars for sodium chloride induced salinity tolerance. *World J. Agric. Sci.,* 4: 574–582.

Munns, R 2002. Comparative physiology of salt and water stress. *Plant cell Environ.,* 25: 239-250.

Munns, R and Tester, M 2008. Mechanisms of salinity tolerance. *Ann. Rev. Plant Biol.* 59: 651-681.

Munns, RA 1993. Physiological processes limiting plant growth in saline soils: Some dogmas and hypothesis. *Plant Cell Environ*., 16**:** 15–24.

Nakamura, T; Liu, Y; Hirata, D; Namba, H; Harada, S; Hirokawa, T and Miyakawa, T 1993. Protein phosphatise type 2B (calcineurin)-mediated, FK506-sensitive regulation of intracellular ions in yeast is an important determinant for adaptation to high salt stress conditions. *EMBO J.,* 12: 4063-4071.

Nautiyal, PC; Bandyopadhyay, A; Koradia, VG and Makad, M 2000. Performance of groundnut germplasm and cultivars under saline water irrigation in the soils of Mundra in Gujarat, India. *Intl. Arachis Newsletter,* 20: 80–82.

Nautiyal, PC; Ravindra, V and Joshi, YC 1989. Germination and early seedling growth of somegroundnut (*Arachis hypogaea* L.) cultivars under salt stress. *Ind. J. Plant Physiol.,* 32: 251–253.

Niu, X; Bressan, RA; Hasegawa, PM and Pardo, JM 1995. Ion Homeostasis in NaCl Stress Environments. *Plant Physiol.*, 109: 735–742.

Noctor, G; Gomez, L; Vanacker, H and Foyer, CH 2002. Interaction between biosynthesis, compartmentation and transport in the control of glutathione homeostasis and signalling. *J Exp Bot.,* 53: 1283–1308.

Nomura, M; Ishitani, M; Takabe, T; Rai, AK and Takabe, T 1995. *Synechococcus sp*. PCC7942 transformed with the *Escherichia coli* bet genes produces glycine betaine from choline and acquires resistance to salt stress. *Plant Physiol.,* 107: 703–708.

Nuccio, ML; Rhodes, D; McNeil, SD and Hanson, AD 1999. Metabolic engineering of plants for osmotic stress resistance. *Curr. Opin. Plant Biol.,* 2: 128-134.

Orcutt, DM and Nilsen, ET 2000. The Physiology of Plants Under Stress: Soil and Biotic Factors. John Wiley and Sons, New York, NY 683 p.

Parida, AK and Das, AB 2005. Salt tolerance and salinity effect on plants: a review. *Ecotoxicol. Environ. Saf.,* 60: 324–349.

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

Passioura, JB and Munns, R 2000. Rapid environmental changes that affect leaf water status induce transient surges or pauses in leaf expansion rate. *Aust. J. Plant Physiol.,* 27: 941–948.

Rathinasabapathi, B; McCue, KF; Gaga, DA and Hanson, AD 1994. Metabolic engineering of glycine betaine synthesis–plant betaine aldehyde dehydrogenases lacking typical transit peptides are targeted to tobacco chloroplasts where they confer betaine aldehyde resistance. *Planta.,* 193: 155–162.

Remorini, D; Melgar, JC; Guidi, L; Degl'Innocenti, E; Castelli, S and Traversi, ML 2009. Interaction effects of root zone salinity and solar irradiance on the physiology and biochemistry of *Olea europaea. Environ Exp.Bot.,* 65: 210–219.

Rezaei, H; Sima, KK; Malakouti, MJ and Pessarakli, M 2006. Salt Tolerance of Canola in Relation to Accumulation and Xylem Transportation of Cations. *J. Plant Nutr.,* 29: 1903–1917.

Rhodes, D and Hanson, AD 1993. Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.,* 44: 357-384.

Romero, C; Bellees, JM; Vaya, JL; Serrano, R and Culianez-Macia, FA 1997. Expression of the yeast trehalose–6-phosphate synthase gene in transgenic tobacco plants: pleiotropic phenotypes include drought tolerance. *Planta,* 201: 293–297.

Rus, A; Yokoi, S; Sharkhuu, A; Reddy, M; Lee, BH; Matsumoto, TK; Koiwa, H; Zhu, JK; Bressan, RA and Hasegawa, PM 2001. *At*HKT1 is a salt tolerance determinant that controls Na+ entry into plant roots. *Proc. Natl. Acad. Sci. USA*, 98: 14150-14155.

Sairam, RK and Tyagi, A 2004. Physiology and molecular biology of salinity stress tolerance in plants. *Curr. Sci.,* 86: 407-421.

Sairam, RK; Rao, VB and Srivastava, GC 2002. Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity, and osmolytes concentration. *Plant Sci.,* 163:1037-1046.

Sairam, RK; Srivastava, GC; Aggarwal, S and Meena, RC 2005. Differences in antioxidant activity in response to salinity stress in tolerant and susceptible wheat genotypes. *Biol. Plant*., 49: 85-91.

Sanders, D 2000. Plant biology: The salty tale of Arabidopsis. *Curr. Biol.,* 10**:** 486-488.

Serrano, R; Culiañez-Maciá, FA and Moreno, V 1999. Genetic engineering of salt and drought tolerance with yeast regulatory genes. *Sci Hortic.,* 78: 261–269.

Sharma, PN; Chatterjee, C; Agarwala, SC and Sharma, CP 1990. Zinc deficiency and pollen fertility in maize (Zea mays). *Plant Soil,* 124: 221–225.

Siddiqui, ZS; Khan, MA; Kim, BJ; Huang, JS and Kwon, TR 2008. Physiological Responses of *Brassica* genotypes to Combined Drought and Salt Stress. *Plant Stress,* 2**:** 78-83.

Siddiqui, ZS; Khan, MA; Kim, BJ; Huang, JS and Kwon, TR 2008. Physiological Responses of *Brassica g*enotypes to Combined Drought and Salt Stress. *Plant Stress,* 2**:** 78-83.

Simond, JM and Orcutt, DM 1988. Free and conjugated desmethylsterol composition of Zea mays hybrids method of determining cold injury. *Plant Physiol.,* 42: 423–1426.

Singh, AL and Chaudhari,V 1993. Screening of groundnut germplasm collection and selection of genotypes tolerant of lime-induced iron-chlorosis. *J. Agric. Sci. Camb*. 121: 205-211.

Singh, AL; Hariprasanna, K and Solanki, RM 2008. Screening of Groundnut Genotypes for Tolerance of Salinity Stress. *Aus. J. Crop Sci.* 1(3): 69-77.

Singh A.L., M.S. Basu and N.B. Singh, 2004. Mineral Disorders of Groundnut. National Research center for groundnut (ICAR), Junagadh India p 85.

Singh, AL; Hariprasanna, K; Chaudhari, V; Gor, HK and Chikani, BM 2010a. Identification of groundnut (*Arachis hypogaea* L.) cultivars tolerant of soil salinity. *J. Plant Nutr.,* 33: 1761-1776.

Singh, A.L., R.S. Jat, Vidya Chaudhari, Himansu Bariya, S.J. Sharma 2010b. Toxicities and Tolerance of Mineral Elements Boron, Cobalt, Molybdenum

and Nickel in Crop Plants. In: Plant Nutrition and Abiotic Stress Tolerance II (Ed: Naser A. Anjum). Plant Stress 4 (Special Issue 2): 31-56, Global Science Books.

Stepien, P and Klobus, G 2006. Water relations and photosynthesis in *Cucumis sativus* L. leaves under salt stress. *Biologia Plantarum,* 50: 610-616.

Sucre, B and Sua´rez, N 2011. Effect of salinity and PEG-induced water stress on water status, gas exchange, solute accumulation, and leaf growth in Ipomoea pes-caprae. *Environ. Exp. Bot.,* 70: 192–203.

Sudhir, P and Murthy, SDS 2004. Effects of salt stress on basic processes of photosynthesis. *Photosynthetica,* 42: 481- 486.

Szabolcs, I 1994. Soils and salinization. In: Handbook of Plant and Crop Stress. Ed. M. Pessarakli, Marcel and Dekker, New York, pp 3-11.

Sze, H; Liang, F; Hwang, I; Curran, AC and Harper, JF 2000. Diversity and regulation of plant Ca^{2+} pumps: insights from expression in yeast. *Ann. Rev. Plant. Physiol. Plant Mol. Biol.,* 51**:** 433-462.

Taiz, L and Zeiger, E 1998. Plant Physiology. Sunderland, Massachusetts: Sinauer Associates, Inc. p. 792.

Takahashi, T and Kakehi, JI 2010. Polyamines: ubiquitous polycations with unique roles in growth and stress responses. *Ann. Bot.,* 105: 1–6.

Tester, M and Davenport, RJ 2003. Na^+ transport and Na^+ tolerance in higher plants. *Ann. Bot.,* 91**:** 503–527.

Thomas, H 1997. Drought resistance in plants. In: Mechanisms of environmental stress resistance in plants, eds. A.S. Basra and R.K. Basra, Amsterdam: Harwood Acad Publishers. pp 1–42.

Tyagi, A; Santha, IM and Mehta, SL 1999. Effect of water stress on proline content and transcript levels in *Lathyrus sativus*. *Ind. J. Biochem. Biophys*., 36**:** 207–210.

Vadez, V; Srivastava, N; Krishnamurthy, L Aruna, R and Nigam, SN 2005. Standardization of a protocol to screen for salinity tolerance in groundnut. *Intl. Arachis Newsletter* 25: 42–47.

Valenzuela, JK; Alvarado, JJ; Sanchez, A and Romero, L 1995. Influence of N, P and K treatments on several physiological and biochemical iron indicators in melon plants irrigated with brackish water. In: Abadıa, J. (Ed.), Iron Nutrition in Soils and Plants. Kluwer Academic Publishers, The Netherlands, pp. 135–140.

van Genuchten, MT and Hoffman, GJ 1984. Analysis of crop salt tolerance data. In: I. Shainberg and J. Shalhevet, eds. Soil salinity under irrigation - process and management ecological studies 51. New York, Springer-Verlag. pp. 258-271.

Vıllora, G; Moreno, DA; Pulgar, G and Romero, L 2000. Yield improvement in zucchini under salt stress: determining micronutrient balance. *Sci. Hort*., 86: 175–183.

Wang, Y and Nil, N 2000. Changes in chlorophyll, ribulose biphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in Amaranthus tricolor leaves during salt stress. *J. Hortic. Sci. Biotechnol*., 75: 623-627.

Watson, R; Pritchard, J and Malone, M 2001. Direct measurement of sodium and potassium in the transpiration stream of salt-excluding and non-excluding varieties of wheat. *J. Exp. Bot.,* 52:1873–1881.

Wimmer MA, Muehling KH, Lauchli A, Brown PH, Goldbach HE (2001) Interaction of salinity and boron toxicity in wheat (*Triticum aestivum* L.). In : Horst WJ, Schenk MK, Burkert A, Claassen N, Flessa H, Frommer WB, Goldbach H, Olfs HW, Romheld V (Eds) *Plant nutrition food security and sustainability of agro ecosystems through basic and applied research, 14th International Plant Nutrition Colloquium,* Hannover, Germany, pp 426-427.

Yahya, A 1998. Salinity effects on growth and on uptake and distribution of sodium and some essential mineral nutrients in sesame. *J. Plant Nutr.,* 21:1439–1451.

Yancey, PH 1994. Compatible and counteracting solutes. In: Strange K, ed. Cellular and molecular physiology of cell volume regulation. Boca Raton: CRC Press, pp. 82–109.

Yeo, AR 1998. Molecular biology of salt tolerance in the context of whole-plant physiology. *J. Exp. Bot*., 49: 915-929.

Yermiyahu U, Ben GA, Keren R, Reid RJ (2008) Combined effect of salinity and excess boron on plant growth and yield. *Plant and Soil,* 304, 73-87.

Yokoi, S; Quintero, FJ; Bressan, RA; Pardo, JM and Hasegawa, PM 2002. Differential expression and function of *Arabidopsis thaliana* NHX Na^+/H^+ antiporters in the salt stress response. *Plant J.,* 30: 529-39.

Zapata, PJ; Serrano, M; Pretel, MT; Amoros, A and Botella, MA 2004. Polyamines and ethylene changes during germination of different plants under salinity. *Plant Sci.,* 167: 781–788.

Zhao, GQ; Ma, BL and Ren, CZ 2007. Growth, gas exchange, chlorophyll fluorescence and ion content of naked oat in response to salinity. *Crop Sci*., 47: 123-131.

Zhu, BC; Su, J; Chang, MC; Verma, DPS; Fan, YL and Wu, R 1998. Over expression of a delta-pyrroline-5-carboxylate synthetase gene and analysis of tolerance to water and salt stress in transgenic rice. *Plant Sci*., 139: 41–48.

Zhu, JK 2001. Plant salt tolerance. *Trends Plant Sci.,* 6: 66-71.

Zhu, JK; Liu, J and Xiong, L 1998a. Genetic analysis of salt tolerance in arabidopsis. Evidence for a critical role of potassium nutrition. *Plant Cell*, 10: 1181–1191.