



## Review article

## Plants responses and their physiological and biochemical defense mechanisms against salinity: A review

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**Abstract:** Plants confront an extent of abiotic stresses due to environmental hardship, among which salinity is one of the major abiotic stresses that seizes plant growth and development resulting in a massive yield loss worldwide. Plants respond to salinity in two distinct phases: a quick osmotic phase and a sluggish ionic phase also known as hyper osmotic phase. Plants adjustment and/or tolerance to salinity stress comprise several complex physiological, biochemical and molecular networks. A widespread understanding of how plants response to salinity stress at different phases, and a cohesive physiological and biochemical approaches are crucial for the development of salt adapted and/or tolerant varieties for salt-affected areas. Researchers have identified several adaptive responses to salinity stress at cellular, biochemical and physiological levels, even though mechanisms triggering salt stress adaptation and/or tolerance are far from being entirely understood. This article bestows a spacious review of foremost research advances on physiological and biochemical mechanisms governing plant adaptation and/or tolerance to salinity stress relevant to environmental sustainability and as well as food production.

**Keywords:** Salinity - Osmotic stress - Ionic stress - Photosynthesis - Reactive oxygen species - Ion homeostasis.

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### INTRODUCTION

Salinity has gained a global concern due to its fierce environmental stresses that inversely influence the growth and development of plants with regulation of metabolic changes (Munns 2002a, Vaidyanathan *et al.* 2003, Munns & Tester 2008). It is categorized by an excessive concentration of soluble salts in growing media, causes significant crop damage globally (Munns & Tester 2008). Today, it is an ascending challenge towards global agriculture to produce 70% more food crop for feeding an addition 2.3 billion souls by 2050 throughout the world (FAO 2009) but this formidable abiotic stress inhibits the agricultural productivity worldwide (Munns & Tester 2008). The problem is constantly rising because of accretion of salt-affected soil day by day which is triggered by various environmental and anthropogenic influences (Boesch *et al.* 1994, Rogers & McCarty 2000). Accumulation of salts over prolonged periods (Rengasamy 2002) due to weathering of parental rocks (Szabolcs 1998) has arisen the maximum salt-affected land naturally. Another reason is the deposition of marine salts transported in wind and rain. Munns & Tester (2008) demonstrated that rain with 10 mg kg<sup>-1</sup> of NaCl would deposit 10 kg ha<sup>-1</sup> of salt for every 100 mm of precipitation for each year. Aloof from natural causes, anthropogenic influences are similarly accountable for soil salinization. Poor quality water in irrigation and global warming with subsequent elevation in sea level and tidal surges, especially in coastal areas are one of the key factors for soil salinization.

Salinity comprises changes in several metabolic and physiological routes, depending on sternness and extent of the stress (Munns 2005). It exerts a devastating effect on plants into two phases. One is the rapid osmotic phase and another is a slower ion toxicity phase. Osmotic phase suppresses the plant/young leaves growth and

development which is then followed by ionic toxicity due to high accumulation of salt in leaves that speeds senescence of mature leaves (Munns 2005, Rahnama *et al.* 2010).

Munns & Tester (2008) suggested plants quench the salt stress challenge *via* three tolerance mechanisms *i.e.* tolerance to osmotic stress, Na<sup>+</sup> exclusion from blades and tissue tolerance whereas McCue & Hanson (1990) suggested four tolerance mechanisms. First is developmental traits, second is structural traits, third is the physiological mechanism and the fourth is metabolic responses, such as modification in photosynthetic metabolism (Cushman *et al.* 1990, Cushman 1992) coupled with biosynthesis of compatible osmolytes and antioxidant enzymes.

An affluent amount of research has been done in demand to understand the mechanism of salinity tolerance in plants (Zhang & Shi 2013) in the previous eras. This current flurry of action may also mirrored that the existing enthusiasms in plant science for building practical support to food production, research progresses on the complex physiological and biochemical mechanisms against salt stress.

## MAGNITUDE OF SALT TOLERANCE IN DIFFERENT CROPS

Salt tolerance ability of every crop is not uniform and differs greatly from crop to crops. The magnitude of salinity tolerance is greater in dicotyledonous species than in monocotyledonous. In cereals, barley is the most tolerant while rice is the most sensitive to salinity (Colmer *et al.* 2006). Moderate tolerance was shown by wheat, bread wheat while durum wheat exhibits less tolerance (Colmer *et al.* 2006). Some legumes are showed moderate tolerance whilst some are very sensitive to salinity. Tall wheatgrass, known as halophytic relative of wheat is one of the most tolerant of the monocotyledonous species (Colmer *et al.* 2006). Halophytes remain to grow well under a quite high concentration of salinity (100–200 mM) (Flowers *et al.* 1977, Bartels 2005).

## PLANTS RESPONSES TO SALT STRESS

### *Germination*

Plant establishment and the yield of the crops depend on seed germination which is a fundamental and crucial phase in the growth cycle of plants. Though seed germination is regulated by a numerous external (environmental) and internal (plant) factors (Wahid *et al.* 2011), a higher level of salt stress adversely affects the seed germination while the lower level of salinity reasons a state of dormancy (Khan & Weber 2008). Seed germination at 80 mM NaCl needs 50% more days whereas it requires almost 100% more days at 190 mM NaCl than control (Cuartero & Fernandez-Munoz 1999). Salinity confines the seed germination and vigor of a several crops species like rice (Xu *et al.* 2011), wheat (Akbarimoghaddam *et al.* 2011), Maize (Carpıcı *et al.* 2009, Khodarahmpour *et al.* 2012), Muatard (Ibrar *et al.* 2003, Ulfat *et al.* 2007), Soybean (Essa 2002), Pulses (Jabeen *et al.* 2003) and Sunflower (Mutlu & Buzcuk 2007).

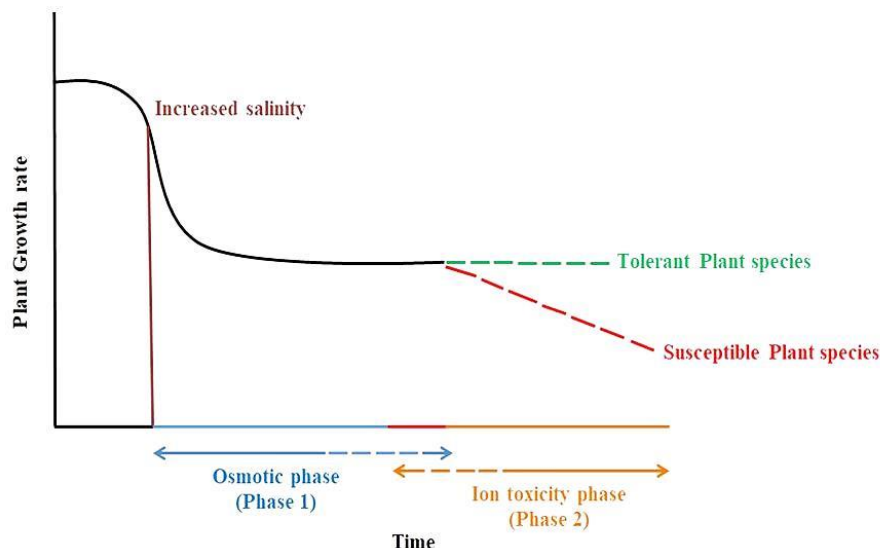
Salinity impairs the imbibition of seeds due to lower osmotic potential (Khan & Weber 2008) which alters the activity of enzymes associated with nucleic acid metabolism (Gomes-Filho *et al.* 2008) and protein metabolism (Yupsanis *et al.* 1994, Dantas *et al.* 2007) leading hormonal imbalance (Khan & Rizvi 1994) and lessens the utilization of seed reserves (Promila & Kumar 2000, Othman *et al.* 2006) thus reduces seed germination. Salt stress is also believed to damage the ultrastructure of cell, tissue and organs (Koyro 2002, Rasheed 2009) that hinder the germination processes.

### *Inhibition of growth parameters*

Cell division and expansion which is mandatory for growth and development is severely affected by salinity (Bursens *et al.* 2000). Munns (2002b) encapsulated the chronological consequences in a plant grown under salinity. He affirmed that the onset of salinity cells is shrunked within first few seconds or minutes, due to loss of water by osmotic stress. Over hours, cells regain their original size but the expansion rates remain low, leading lower growth rates of leaf, shoot and root. Across days, it affects cell division rate and responsible for lower leaf, shoot and root growth rates. After several weeks, it alters the vegetative development and fluctuations in reproductive development can be seen over months. Later on, Munns and Tester (2008) established the two-phase growth response model for well understanding the responses of plants to salinity (Fig. 1).

The first phase is a rapid process which is due to osmotic effect begins instantly after an increase of salt concentration around the roots to a threshold level (approximately 4 dsm<sup>-1</sup> NaCl or less for sensitive plants like rice and Arabidopsis) (Munns & Tester 2008). This phase is documented as osmotic stress phase. The second phase is a slower process which is due to the accumulation of salt to toxic concentrations in the old leaves (which do not expand and so no longer diluting the salt inward in them as younger developing leaves do) leading to ionic toxicity in the plants (Munns & Tester 2008). This phase is documented as ionic toxicity phase

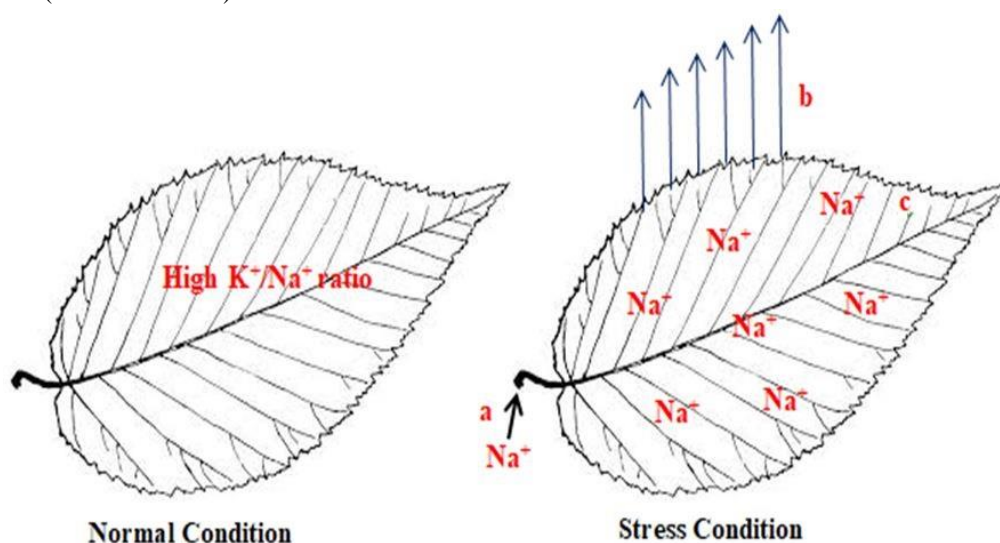
or hyperosmotic stress phase. Ionic toxicity causing from distorted  $K^+/Na^+$  ratio and deposition of  $Na^+$  and  $Cl^-$  ion in leaves over an extended period of time after transpiration, results in injury and/or death of leaves and decrease the total photosynthetic leaf area which lower the supply of photosynthate in plants and finally alter the productivity. Leaf injury and/or death are documented to the elevated salt load in the leaf that exceeds the capability of salt compartmentalization in the vacuoles, that results in the cytoplasm toxic (Munns 2002a, 2005, Munns *et al.* 2006). Beneath such condition, a plant eventually may die (Blaylock 1994).



**Figure 1.** An outline of two phase growth response against salt stress. (Modification of Munns & Tester 2008)

**Accumulation of  $Na^+$  ions**

During salinity,  $Na^+$  accumulation is a common phenomenon in leaves rather than in the roots after being deposited from the transpiration steam (Amtmann & Sanders 1998, Munns 2002a). In standard physiological circumstances, plants maintain a high  $K^+/Na^+$  ratio in their cytosol (Binzel *et al.* 1988) but an elevation in extracellular  $Na^+$  concentrations occurs due to the negative electrical membrane potential at the plasma membrane (-140 mV) (Higinbotham 1973) that favors the passive transportation of  $Na^+$  ions into cytosol from the environment and deposits into leaf cell after transpiration (Fig. 2). The extreme  $Na^+$  in the cytosol has been exhibited poor survival of plants and eventually death as well (Krishnamurthy *et al.* 2009).  $Na^+$  ions restrict the function of potassium which performances as a cofactor in several reactions and hence exhibits direct toxicity on the plant. In addition  $Na^+$ , however, seems to be detrimental to the structural and functional integrity of membranes (Iraki *et al.* 1989).

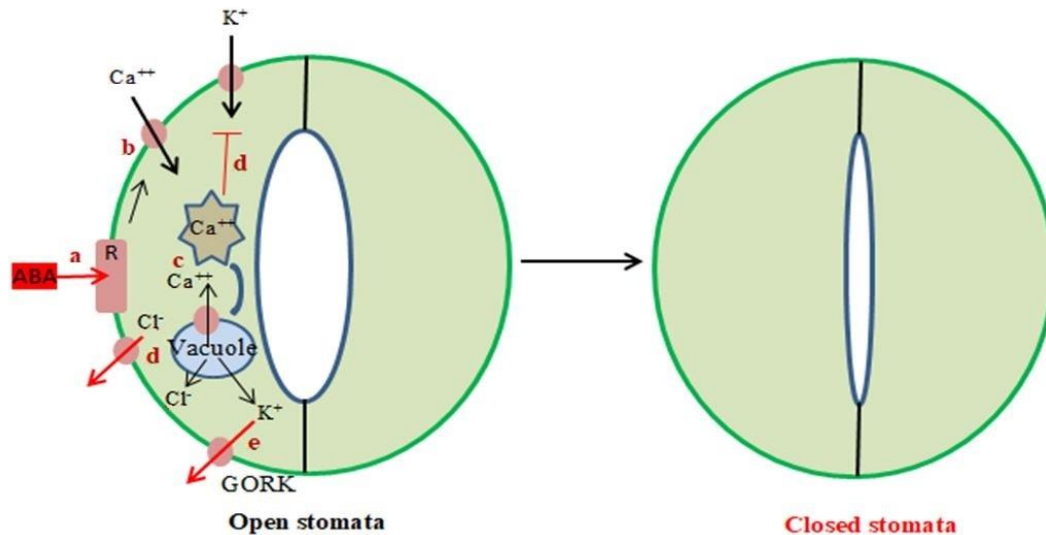


**Figure 2.** Accumulation of  $Na^+$  ions. Where, a- Passive transportation of  $Na^+$  due to the negative electrical membrane potential; b- Water loss from leaf by transpiration; c- Deposition and/or accumulation of  $Na^+$  in leaf cell.

**Stomatal closure**

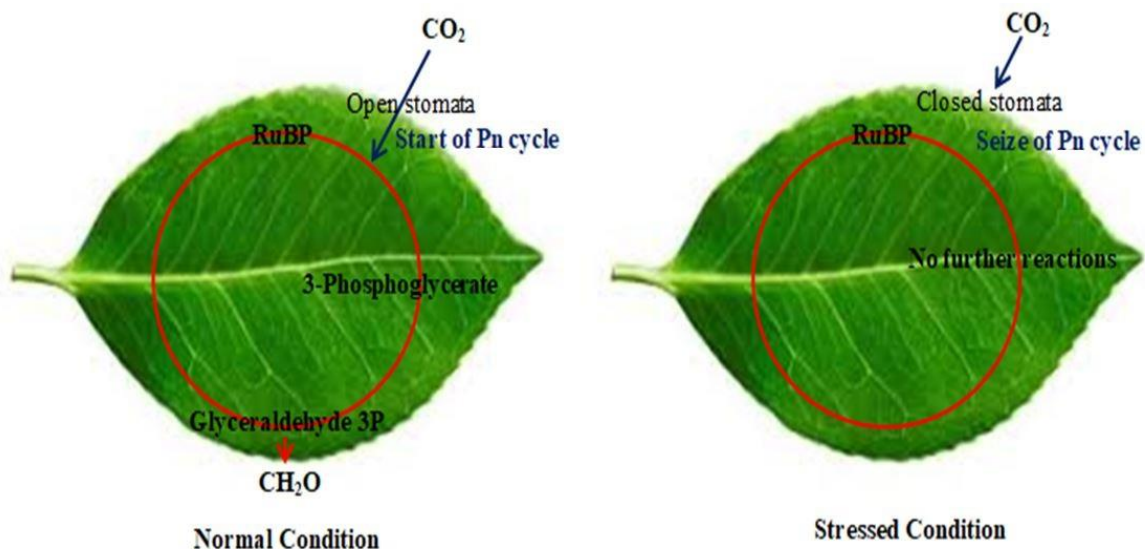
A further response of plants to salinity is demonstrated by a reduction in stomatal aperture which is believed to induce by the osmotic effect. Salinity disturbs stomatal conductance rapidly and transiently due to interrupt in [www.tropicalplantresearch.com](http://www.tropicalplantresearch.com)

water relations and sharply the local synthesis of short-lived ABA in roots (Fricke 2004) and immediately relocate into the leaves through xylem. ABA then fixes with plasma membrane receptor molecule of guard cells and this fixation trigger activation of  $\text{Ca}^{2+}$  channel proteins which inflows  $\text{Ca}^{2+}$  into the cytosol from outside. Simultaneously activation  $\text{Ca}^{2+}$  channels present on tonoplast starts to efflux of  $\text{Ca}^{2+}$  in cytosol from the vacuole, leads to further rise in  $\text{Ca}^{2+}$  in the cytosol. High  $\text{Ca}^{2+}$  concentration inhibits  $\text{K}^+$  channel proteins activity though it keeps normal  $\text{Cl}^-$  channel proteins activity. Consequently, no  $\text{K}^+$  is influxed and efflux of  $\text{Cl}^-$  from cytosol initiates to enhance cytosolic pH cause depolarization of plasma membrane. At existing circumstances,  $\text{K}^+$  (known as water buoy) is effluxed through Guard Cell Outward Rectifying  $\text{K}^+$  (GORK) channel triggering lose in turgidity in guard cell and cause stomatal closure (Blatt & Armstrong 1993) (Fig. 3).



**Figure 3.** ABA mediated stomatal closure. Where, a- ABA binds with PM receptor molecule; b- Boost  $\text{Ca}^{2+}$  channel protein to influx  $\text{Ca}^{2+}$  in cytosol; c- Simultaneous  $\text{Ca}^{2+}$  efflux in cytosol from vacuole leads further raise in  $\text{Ca}^{2+}$ ; d- Increased  $\text{Ca}^{2+}$  inhibit the activity of  $\text{K}^+$  inward channel while keeps normal the  $\text{Cl}^-$  channel activity causing depolarization of plasma membrane; e- This situation facilitates removal of  $\text{K}^+$  from guard cell through GORK channel causing stomatal close. (Modification of outline of Blatt & Armstrong 1993)

#### Inhibition of Photosynthesis



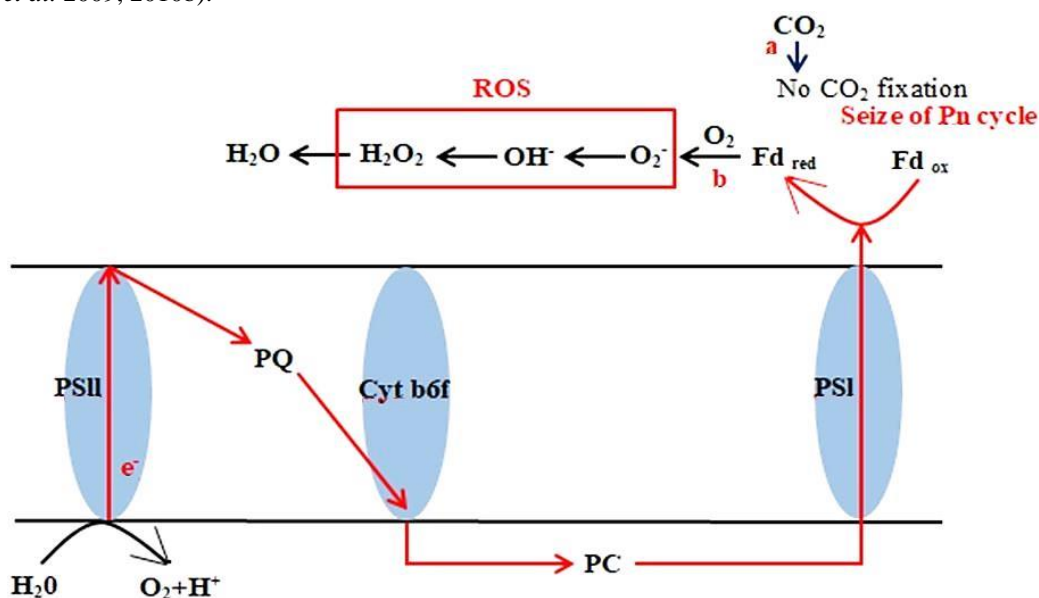
**Figure 4.** General reactions of photosynthesis and inhibition of photosynthesis during salt stress.

Salt stress is believed to be responsible for lower photosynthesis which is triggered by ABA mediated stomatal closure. The diminution in stomatal conductance inhibits the accessibility of  $\text{CO}_2$  for carboxylation reactions in leaves that decreases photosynthesis under stress (Brugnoli & Björkman 1992) (Fig. 4). Besides, one of the most noted effects of salinity that reduces the photosynthesis is the variation in biosynthesis of photosynthetic pigment (Maxwell & Johnson 2000). The reduction in Chlorophyll content under salt stress is a normally stated phenomenon (Chutipaijit *et al.* 2011). Chutipaijit *et al.* (2011) demonstrated that subjected to 100 mM NaCl showed 30, 45 and 36% reduction in Chlorophyll a (Chl a), Chlorophyll b (Chl b) and carotenoids (Car)

contents respectively as compared to control in rice. Photosynthesis is also obstructed when excessive concentrations of  $\text{Na}^+$  and/or  $\text{Cl}^-$  are amassed in chloroplasts.

### Oxidative stress

Salinity invites oxidative stress through a series of actions. It triggers stomatal closure, leading decreases  $\text{CO}_2$  availability for carbon fixation in the leaves, unmasking chloroplasts to extreme excitation energy which in turn rise the generation of reactive oxygen species (ROS) such as superoxide ( $\text{O}_2^-$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), hydroxyl radical ( $\text{OH}^\cdot$ ) and singlet oxygen ( $^1\text{O}_2$ ) (Apel & Hirt 2004, Foyer & Noctor 2005a, Parida & Das 2005, Ahmad & Sharma 2008, Ahmad *et al.* 2010a, 2011) that initiate programmed cell death (Jacobson *et al.* 1997, Jabs, 1999, Gunawardena *et al.* 2004) (Fig. 5). On the other hand, physiological water deficit because of osmotic effect alters a wide range of metabolic activities (Greenway & Munns 1980, Cheeseman 1988) leads to the generation of ROS (Halliwell & Gutteridge 1985, Elstner 1987). ROS are extremely reactive and may reason cellular damage through lipid peroxidation as well as proteins and nucleic acids oxidation (Hasegawa *et al.* 2000, Pastori & Foyer 2002, Apel & Hirt 2004, Ahmad *et al.* 2010a, 2010b) demonstrated that generation of ROS is enhanced under saline conditions and ROS-mediated membrane destruction has been revealed to be a foremost reason of the cellular toxicity in several crop plants such as rice, tomato, citrus, pea and mustard (Gueta-Dahan *et al.* 1997, Dionisio-Sese & Tobita 1998, Mittova *et al.* 2004, Ahmad *et al.* 2009, 2010b).



**Figure 5.** An overview of oxidative stress during salinity stress. Where, a- No  $\text{CO}_2$  fixation due to stomatal closure; b- Initiation of ROS generation *via.* mehlhar reaction.

### Nutrient imbalance

High salt concentration due to salinity is believed to cause nutrient imbalance. A number of reports showed that salinity decreases nutrient uptake and accumulation of nutrients into the plants (Rogers *et al.* 2003, Hu & Schmidhalter 2005). Rozeff (1995) demonstrated that salinity lower N accumulation in plants due to the interaction between  $\text{Na}^+$  and  $\text{NH}_4^+$  and/or between  $\text{Cl}^-$  and  $\text{NO}_3^-$  that finally lessen the growth and yield of the crop. Plants face phosphorus (P) deficiency in saline soils due to ionic strength effects that decreased the activity of  $\text{PO}_4^{3-}$  and low solubility of Ca-P minerals. Elevated level of  $\text{Na}^+$  ion concentrations in the soil decreases the quantity of available  $\text{K}^+$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  (Epstein 1983) hence, directing to nutrient imbalance. The solubility of micronutrients, pH of soil solution, redox potential of the soil solution and the nature of binding sites on the organic and inorganic particle surfaces are the principal factors for the availability of micronutrients in saline soils. Zhu *et al.* (2004) reported that micronutrient deficiencies are common in salt stress because of high pH.

### Plant yield

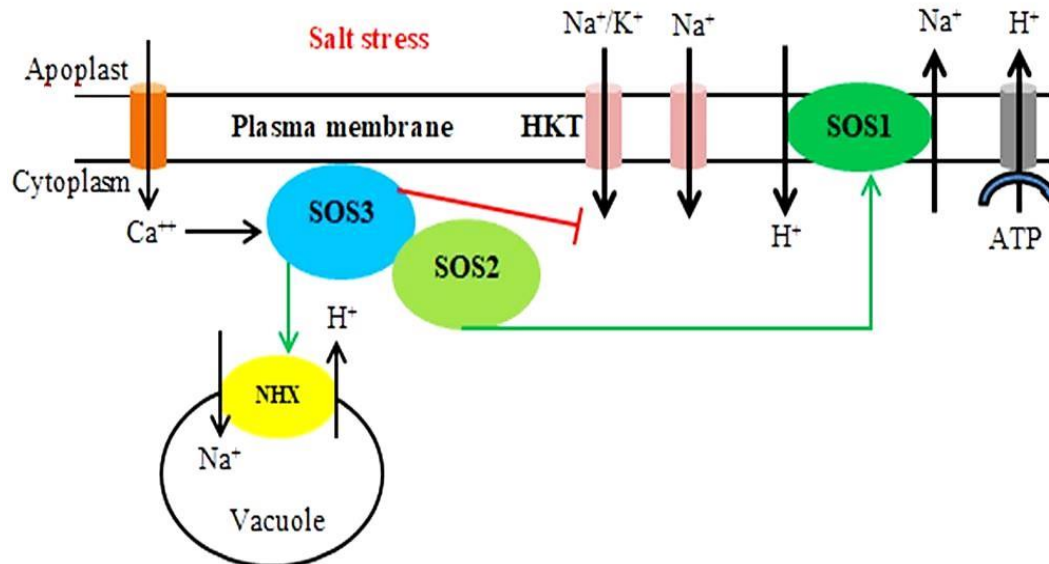
The above-stated responses against salt stress lead to the diminution of crop yield which is the most noticeable effect in agriculture. Salinity causes great crops reduction and yields almost all plant species except some halophytes. Nahar & Hasanuzzaman (2009) showed an application of 250 mM NaCl decreased 77, 73 and 66% yield in BARI mung-2, BARI mung-5 and BARI mung-6, respectively over control. Later on Hasanuzzaman *et al.* (2009) demonstrated that at 150 mM salinity BR11, BRRI dhan41, BRRI dhan44 and

BRR1 dhan46 showed loss of grain yield at 50, 38, 44 and 36% respectively over control. Greenway & Munns (1980) observed that at 200 mM NaCl, sugar beet (a salt-tolerant species) might have a reduction of only 20% in dry weight, cotton (a moderately tolerant) might have a 60% reduction, and as a sensitive species soybean might be dead. In contrast, a halophyte such as *Suaeda maritima* (L.) might be growing at its optimum rate under salinity (Flowers *et al.* 1986). This reduction of yield and yield components under salt stress may also be assigned to low cell expansion, less photosynthetic rate, senescence and production (Seemann & Critchley 1985, Wahid *et al.* 1997).

## PHYSIOLOGICAL AND BIOCHEMICAL BASIS OF SALT TOLERANCE

### Ion Homeostasis and compartmentalization

Ion homeostasis and compartmentalization is not only indispensable for normal plant growth but is also a crucial process for growth and development under salt stress (Niu *et al.* 1995, Serrano *et al.* 1999, Hasegawa 2013). Though halophytes can accept high salt concentration during their growth and development, irrespective of their nature, glycophytes cannot tolerate an elevated concentration of salt in their cytoplasm. Hence, the additional salt is either sequestered in older tissues which finally are sacrificed or conveyed to the vacuole; thereby defending the plant from salinity stress (Reddy 1992, Zhu 2003). NaCl is the most abundant form of salt existing in the soil, so the main importance should be given about the transport mechanism and compartmentalization of  $\text{Na}^+$  ion. Cytoplasmic  $\text{Na}^+$  ion is moved to the vacuole *via*.  $\text{Na}^+/\text{H}^+$  antiporter. Vacuolar type  $\text{H}^+$ -ATPase (V-ATPase) and vacuolar pyrophosphatase (V-PPase) are two types of  $\text{H}^+$  pumps located in the membrane of vacuolar (Dietz 2001) responsible for ion homeostasis and compartmentalization. Between them, V-ATPase is the most dominant  $\text{H}^+$  pump plays a significant role in both stressed and non-stressed conditions. Under stressed condition, the survivability of the crops/plants greatly depend upon the action of V-ATPase whereas it helps to maintain solute homeostasis, stimulating secondary transport and assisting vesicle fusion in non-stressed (Dietz 2001, De Lourdes Oliveira Otoch *et al.* 2001, Wang 2001). De Lourdes Oliveira Otoch *et al.* (2001) observed enhanced functions of V-ATPase pump and suppressed activity of V-PPase pump in hypocotyls of cowpea seedlings under salt stress environment whereas in halophyte *Suaeda salsa* (L.) Pall. (seepweeds), V-ATPase activity was upregulated and V-PPase played a minimal role (Wang 2001).



**Figure 6.** Model of SOS pathway for ion homeostasis and compartmentalization during salt stress. (Modification of outline of Gupta & Huang 2014)

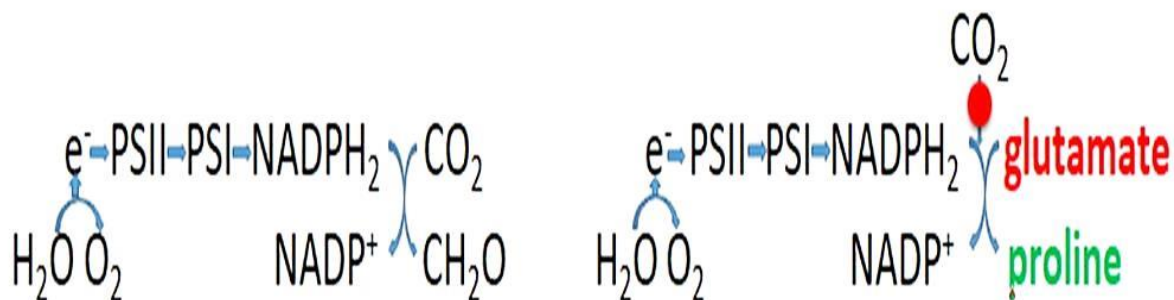
Salt Overly Sensitive (SOS) stress signaling pathway is also responsible for ion homeostasis and salt tolerance (Hasegawa *et al.* 2000, Sanders, 2000). SOS consists of three major proteins: a) SOS1 protein that encodes a plasma membrane  $\text{Na}^+/\text{H}^+$  antiporter, is crucial in controlling  $\text{Na}^+$  efflux at cellular level. Besides, long distance transport of  $\text{Na}^+$  from root to shoot is assisted by SOS1. Overexpression of this SOS1 protein bestows salt tolerance in plants (Shi *et al.* 2000, Shi *et al.* 2002); b) SOS2 protein that encodes serine/threonine kinase and consists of a well-developed N-terminal catalytic domain and a C-terminal regulatory domain (Liu *et al.* 2000). SOS2 is activated by the action of both SOS3 protein and salt stress elicited  $\text{Ca}^{2+}$  signals; c) Another protein in SOS signaling pathway is the SOS3 protein which is a myristoylated  $\text{Ca}^{2+}$  binding protein along with a myristoylation site at its N-terminus. This myristoylation site shows a crucial role in salt tolerance (Ishitani *et*

*al.* 2000). C-terminal regulatory domain of SOS2 protein performs as a site of interaction for  $\text{Ca}^{2+}$  binding SOS3 protein resulting in the initiation of the kinase (Guo *et al.* 2004). The activated kinase then phosphorylates SOS1 protein thus escalating its transport activity *via.*  $\text{Na}^+/\text{H}^+$  antiporter (Quintero *et al.* 2002). This result increase  $\text{Na}^+$  efflux and thus ease  $\text{Na}^+$  toxicity (Martinez-Atienza *et al.* 2007) (Fig. 6).

#### **Compatible solute accumulation and osmotic protection**

Biosynthesis and/or accumulation of compatible solutes are inhabitable in stress condition. They are uncharged, polar, and soluble in nature and do not interfere with the cellular metabolism even at high concentration. The well documented compatible solutes found in are proline (Pro) (Ashraf & Foolad 2007, Hoque *et al.* 2007, Ahmad *et al.* 2010a, Nounjan *et al.* 2012, Tahir *et al.* 2012), glycinebetaine (GB) (Khan *et al.* 2000, Wang & Nii 2000, Ashraf & Foolad 2007), sugar (Bohnert *et al.* 1995, Kerepesi & Galiba 2000), and polyols (Ford 1984, Ashraf & Foolad 2007, Saxena *et al.* 2013) As their biosynthesis and/or accumulation is associated to the external osmolarity, the major functions of these osmolytes is to shield the structure of cells and to maintain osmotic balance thru continuous water influx (Hasegawa 2013). Besides, an inorganic osmolyte recognized as  $\text{K}^+$  plays an important role in osmoregulation thus salinity mitigation (Shabala 2003, Polash *et al.* 2018)

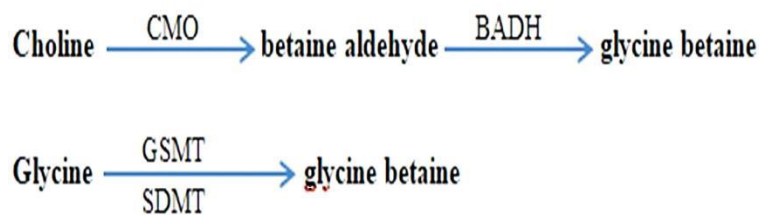
**Proline:** Proline (Pro) biosynthesis and/or accumulation are a well-known phenomenon for decreasing salinity stress (Matysik *et al.* 2002, Ben-Ahmed *et al.* 2010, Saxena *et al.* 2013). In osmotically stressed cell Pro is synthesised either from glutamate or ornithine (Fig. 7). The biosynthetic pathway includes two major enzymes; a) pyrroline carboxylic acid synthetase and b) pyrroline carboxylic acid reductase, which are responsible for overproduction of Pro in plants under stress (Sairam & Tyagi 2004). Nounjan *et al.* (2012) observed that salt stress resulted in growth reduction, increase in the  $\text{Na}^+/\text{K}^+$  ratio, increase in Pro level and up-regulation of proline synthesis gene as well as accumulation of  $\text{H}_2\text{O}_2$ , increased activity of antioxidative enzymes (SOD, POX, APX, CAT) of rice seedlings. Intracellular Pro provides tolerance toward stress and also behaves as an organic nitrogen reserve during stress recovery. Pro assists in stimulating the expression of salt-stress-responsive proteins (Khedr *et al.* 2003) acts as an antioxidant feature, suggesting ROS scavenging activity and  $^1\text{O}_2$  quencher, protects the photosynthetic apparatus (Ashraf *et al.* 2008) thus develop the plant adaptation against salt stress (Smirnoff & Cumbes 1989, Matysik *et al.* 2002). Deivanai *et al.* (2011) demonstrated that pretreatment with 1 mM Pro exhibited advance in growth during salt stress in rice seedlings. It has been demonstrated by a study that Pro increases salt tolerance in tobacco by intensifying the activity of enzymes participating in antioxidant protection system (Hoque *et al.* 2008). Antioxidant enzyme activity such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) is significantly inhibited by salt which is upregulated by Pro supplements. Ahmad *et al.* (2010b) observed in olive trees, that Pro supplements appeared to improve salt stress tolerance by regulating antioxidant enzymatic activities, enhancing the photosynthetic activity, and thus preserved well plant growth and water influx. Besides the exogenous application of Pro significantly mitigate the reduction of photosynthesis (Pn), fluorescence (Fv/Fm), and chlorophyll (Chl) content under saline conditions. Nounjan *et al.* (2012) reported that exogenous supplementation of Pro repressed the  $\text{Na}^+$  induced apoplasmic flow thus reduce  $\text{Na}^+$  uptake in rice. They also demonstrated that application of Pro to the salt stress environment repressed Na-induced trisodium-8-hydroxy-1,3,6-pyrenetrisulphonic acid uptake and  $\text{Na}^+$  accumulation, whereas the  $\text{K}^+$  content was fairly increased, leading to a high  $\text{K}^+/\text{Na}^+$  ratio under salt stress.



**Figure 7.** Biosynthesis of Pro from glutamate during salinity. (Modification of Hossain *et al.* outline 2011a)

**Glycinebetaine:** Glycinebetaine (GB) is an amphoteric quaternary ammonium compound and non-toxic even at higher concentrations in cell which plays a defensive role to salt stress (Ashraf & Foolad 2007, Chen & Murata 2008). The most common pathway of GB synthesis from choline is a two-step reaction, first choline

is oxidized to betaine aldehyde catalyzed by choline monoxygenase (CMO) which is further undergoes oxidation to form glycine betaine by the activity of betaine aldehyde dehydrogenase (BADH) (Ahmad *et al.* 2013) (Fig. 8). Another pathway of synthesis involves three successive N-methylation which are catalyzed by, glycine sarcosine N-methyl transferase (GSMT), and sarcosine dimethylglycine N-methyl transferase (SDMT) (Ahmad *et al.* 2013). The foremost roles of glycinebetaine are shields the cell by stabilizing protein (Mäkelä *et al.* 2000), osmotic adjustment (Gadallah 1999), defends the photosynthetic apparatus from stress injuries (Cha-Um & Kirdmanee 2010) and reduction of ROS (Ashraf & Foolad 2007, Saxena *et al.* 2013). Rahman *et al.* (2002) demonstrated the positive effect of GB on rice seedlings when uncovered to salt stress. The affirmative effect of exogenous application of GB is related with reduced  $\text{Na}^+$  accumulation along with the maintenance of higher  $\text{K}^+$  concentration within all parts of salt-stressed plants. This effect might be due to the creation of numerous vacuoles in the root cells in which  $\text{Na}^+$  is stored and prevent its accumulation in the shoots. Cha-Um & Kirdmanee (2010) applied GB on salt-sensitive rice plants bared to 150 mM of NaCl stress. The results revealed that GB treated plants exhibited higher water use efficiency (WUE) and pigment stabilization, leading to high  $\text{CO}_2$  assimilation, photosynthetic performance as well as plant height under salinized environment.



**Figure 8.** Biosynthesis of GB from choline during salinity.

**Trehalose:** Trehalose (Tre) another compatible osmolyte documented in plants during stress functions as an osmoprotectant increasing the plant's tolerance to abiotic stress (Zeid 2009, López-Gómez & Lluch 2012). Nounjan *et al.* (2012) monitored the reduction of  $\text{Na}^+/\text{K}^+$  ratio in rice seedlings under salt stress condition when treated with exogenous Tre. Another experiment demonstrated that pre-treatment of maize seeds with Tre (10 mM) exhibited better functions under salt stress environment (Zeid 2009). Tre application also believed to ease salt stress over stabilization of plasma membranes, photosynthetic pigments by declining ion leakage rate, and boosting the ratio of  $\text{K}^+/\text{Na}^+$  in the leaves of stressed plants. However, the exogenous role of Tre in mitigating growth inhibition under abiotic stress is still under examination. Further investigations are needed for advance understanding about the role of Tre in crop protection under salinity.

**Polyols:** Polyols consists of several hydroxyl functional groups, functions as a compatible solute that stabilizes the enzymes and scavenges ROS (Ashraf & Foolad 2007) under salt stress conditions. They are categorized into acyclic (*e.g.* mannitol) and cyclic (*e.g.* pinitol) groups. Mannitol biosynthesis occurs in plants through activity of NADPH dependent mannose-6-phosphate reductase under stressed period. Pinitol is also biosynthesized within the cell when the plant is exposed to salinity. Pinitol biosynthetic pathway involves of two major phases: first formation of ononitol due to the methylation of myoinositol and then epimerization ononitol to produce pinitol by the action of inositol methyl transferase enzyme. However, accumulation of polyols in plants is correlated with tolerance to drought and/or salinity (Bohnert *et al.* 1995).

**Carbohydrates:** Carbohydrates such as sugars (*e.g.* glucose, fructose, fructans, and trehalose) and starch accumulation occur under salt stress condition (Parida *et al.* 2004). These carbohydrates is well documented in osmoprotection, carbon storage and scavenging of ROS in stress mitigation. Kerepesi & Galiba (2000) detected the escalation of reducing sugars (sucrose and fructans) within the cell under salinized environment in a number of plants species. In another study, the sucrose content was found to enhance in tomato under salinity by increased activity of sucrose phosphate synthase (Gao *et al.* 1998). On the other hand, sugar content, has been reported to both enhance and decline in various rice genotypes under salinity (Alamgir & Ali 1999). However, advanced studies are required to reveal the proper mechanisms of carbohydrates against salinity alleviation.

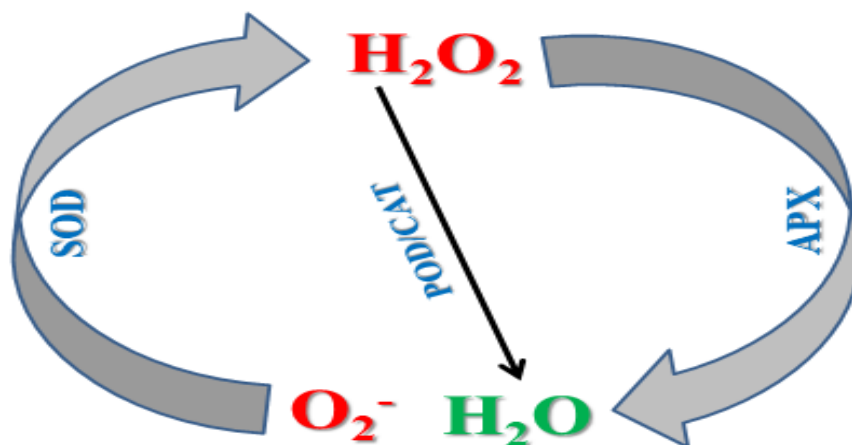
**Inorganic osmolytes ( $\text{K}^+$ ) in osmoregulation under salinity:** Some studies revealed that, inorganic osmolyte exhibits an important role in salt stress adaption and/or tolerance rather organic osmolytes (Shabala 2003, Polish *et al.* 2018). According to Hanson *et al.* (1977) and Moftah & Miche (1987), Pro biosynthesis is not always rapid and might not have occurred till the cells are damaged fatally. In this circumstance,  $\text{K}^+$  an



inorganic osmoticum involves in retaining water content as well as cell turgidity by maintaining ionic balance (Shabala 2003).

### **Antioxidant Regulation of Salinity Tolerance**

**SOD, APX, CAT and POD:** Deregulation and interruption of electron transport chains (ETC) leads overflow of electron in chloroplasts and mitochondria initiate several abiotic and biotic stresses both in living animals and plants. Under such environment, molecular oxygen ( $O_2$ ) performances as an electron acceptor, triggers production of ROS *via*. mehlhar reaction (Asada 1999). ROS are strongly oxidizing compounds that are injurious for cell integrity (Groß *et al.* 2013). In this context, antioxidant enzymatic and non-enzymatic compounds play critical function in detoxifying ROS induced by salinity stress. Biosynthesis and/or accumulation of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR) is believed to positively reduce the salinity stress (Asada 1999, Gupta *et al.* 2005). SOD commences the process of ROS detoxification by converting super oxide to hydrogen peroxide (Alscher *et al.* 2002, Hernandez *et al.* 2009, Jalali-e-Emam *et al.* 2011) this hydrogen peroxide further convert into oxygen and water to remove the peroxide in plants due action of CAT (Ho *et al.* 1998). Similar results are also demonstrated by Nounjan *et al.* (2012) on rice and Manivannan *et al.* (2007) on mung bean. APX antioxidant activity is increased with the increase of NaCl concentration, in all the plants species under salt which was supported by (Turan & Tripathy 2013) and (Weisany *et al.* 2012) on soybean plant but Ozturk *et al.* (2012) reported the reduction in APX activity in pea plant. APX play a key role in the conversion of  $H_2O_2$  into  $H_2O$ , using ascorbate as a specific electron donor (Caverzan *et al.* 2012, Hossain & Fujita 2013). Salt stress has a significant effect on POD activity. Almost all the plants exhibited increasing response in POD activity under salinity stress which were reported by Sajjad *et al.* (2012) in rape cultivars, Weisany *et al.* (2012) in soybean and Shaheen (2013) in eggplant. It is believed that, peroxidase in cytosol and peroxisomes efficiently eliminate  $H_2O_2$  found outside the chloroplast (Asada 1992) (Fig. 9).



**Figure 9.** Antioxidant regulation in salt stress alleviation.

**Ascorbic acid:** Ascorbic acid (Vitamin C) also known as ascorbate (AsA) is one of the most important antioxidant in plant which is manufactured in cytosol of higher plants by conversion of d-glucose. Besides assists in numerous physiological developments including growth, differentiation and metabolism in plants, AsA significantly eliminates free radicals, thus lessening the impairment caused by oxidative stress (Shigeoka *et al.* 2002, Foyer 2004, Foyer & Noctor 2005a, 2005b). AsA further assists in membrane protection (Li & Jin 2007) and also acts a co-factor of violaxanthin de-epoxidase, thereby supports in dissipation of excess excitation energy (Pource *et al.* 2007). Several studies found an elevation level of AsA content in the leaves of stressed plants over control (Panda & Upadhyay 2004, Parida *et al.* 2004, Agarwal & Shaheen 2007, Mohamed *et al.* 2010). AsA induced enhancement in the growth of salt-stressed plants coupled with an increase in CAT, POD and SOD activities (Munir & Aftab 2011). Exogenous application of AsA facilitates many enzyme activities and decreases the injury caused by oxidative processes (Shalata & Neumann 2001, Athar *et al.* 2008). Tomato seedling treated with exogenous AsA helps to reduce lipid peroxidation thus recovers plants from salt stress (Shalata & Neumann 2001). Later on Hamada & Al-Hakimi (2009) stated the role of exogenous application of AsA in countering the inverse effects of salt stress on membrane integrity, pigments biosynthesis and net photosynthetic rate in sun flower plants. However,

salt-induced drop in leaf Chl a and b concentrations in chili was enhanced with AsA pre-treatment (Khafagy *et al.* 2009). A study by Azzedine *et al.* (2011) described that the exogenous application of AsA was helpful to alleviate the negative effect of salt stress on plant growth by increasing leaf area, enriching Chlorophyll and Carotene contents, boosting Pro accumulation and declining H<sub>2</sub>O<sub>2</sub> content.

**Glutathione:** Glutathione (GSH) is another strong antioxidant documented in plants which counteracts the damage of principal cellular components due to ROS generation (Pompella *et al.* 2003). GSH also defends proteins from denaturation and function as a substrate for glutathione peroxidase (GPX) and glutathione-S-transferases (GST), which regulates in the removal of ROS (Noctor *et al.* 2002). It also contributes in regeneration of ascorbate *via* ascorbate-glutathione cycle (Foyer *et al.* 1997). A study by Aly-Salama & Al-Mutawa (2009) reported that exogenous application of glutathione helped to maintain plasma membrane permeability and cell viability under salt stress in onion. Combined application of glutathione and ascorbate assists in increasing morphological parameters, antioxidant activity and mineral ion content while exposed to salinized environment (Rawia *et al.* 2011).

**Tocopherols:** Tocopherols are amphiphilic antioxidants belong to the family of vitamin E also found in plants in stress mitigation. Tocopherols are known to reduce the ROS levels in photosynthetic membranes and restricts the extent of lipid peroxidation thru decreasing lipid peroxy radicals (LOO<sup>•</sup>) (Maeda *et al.* 2005, Munné-Bosch 2005). Rady *et al.* (2011) demonstrated that exogenous  $\alpha$ -tocopherol application enhanced total soluble sugars content and the activities of CAT, POX, PPO and PAL under salt stress. Pre-treatment with  $\alpha$ -tocopherol also enriched the mineral nutrient content in the plant with simultaneous increase in Pro, total phenols and free amino acids. Application of  $\alpha$ -tocopherol helps to reduce salt-induced leaf senescence by decreasing the Na<sup>+</sup> and Cl<sup>-</sup> content and increasing the K<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> contents (Farouk 2011). In addition, tocopherols involve in ROS, antioxidants, and phytohormones mediated signaling network thereby maintain cellular signaling in plants (Munné-Bosch 2007).

#### **Roles of polyamines in salinity tolerance**

Polyamines (PAs) are small and poly cationic aliphatic molecules with low molecular weight found in entire the plant kingdom. Besides its functions in normal growth and development, dormancy breaking and germination, improvement of flowers and fruits, and senescence (Galston *et al.* 1997, Panicot *et al.* 2002, Knott *et al.* 2007, Gupta *et al.* 2013a). PAs are related with stress tolerance in plants (Yang *et al.* 2007, Groppa & Benavides 2008, Gupta *et al.* 2013b). The most familiar and documented PAs within the plants are diamine putrescine (PUT), triamine spermidine (SPD) and tetra-amine spermine (SPM) (Martin-Tanguy 2001, Kuznetsov & Shevyakova 2007, Alcazar *et al.* 2006, 2010a, 2010b, Hussain *et al.* 2011, Shu *et al.* 2012). Among them, PUT is the smallest PAs and is originated from either ornithine or arginine with the assistance of ornithine decarboxylase (ODC) and arginine decarboxylase (ADC) enzyme respectively (Gupta *et al.* 2013b, Hasanuzzaman *et al.* 2014). The triamine SPD and tetramine SPM are produced by successive addition of amino propyl group with PUT and SPD, respectively, which is catalyzed by spermidine synthase (SPDS) and spermine synthase (SPMS) (Fluhr *et al.* 1996, Alcazar *et al.* 2006). The significant roles of PAs have been documented with alteration of gene expression for the biosynthesis and/or accumulation of osmotically active solutes, maintenance of membrane integrity, better photosynthetic efficiency, drop in ROS generation and accumulation of Na<sup>+</sup> and Cl<sup>-</sup> ion in different organs (Navakoudis *et al.* 2003, Roy *et al.* 2005, Tisi *et al.* 2008, Duan *et al.* 2008, Afzal *et al.* 2009, Roychoudhury *et al.* 2011) in salinized environment. Recently several studies have been stated that PAs functions as cellular signals associated with ABA hormonal pathways (Alcazar *et al.* 2010a, 2010b, Gill & Tuteja 2010). Tun *et al.* (2006) reported that, PAs like SPM and SPD are related to potent inducers of NO, which is acknowledged as another potent signaling molecule in plants.

Moreover, exogenous application of PAs has been discovered to boosts the level of endogenous polyamine during stress. It has been reported by Duan *et al.* (2008) and Liu *et al.* (2006) that, exogenous treatment of PAs improves salt-induced fall in photosynthetic efficacy though their effect is soundly associated with both concentration and strength of stress levels. Amri *et al.* (2011) presented that; application of exogenous PAs with different concentrations may assist to alleviate the detrimental effects of salt stress on growth and development of pomegranate. Exogenous Put significantly reduced the Na<sup>+</sup> and Cl<sup>-</sup> accumulation in shoots and roots, membrane damage and enhanced RWC, pigments content thus photosynthetic rate in salt-treated *Citrus aurantium* L. (Sharma *et al.* 2011). Exogenous SPD to nutrient solution resulted in improvement of the salt-induced growth reduction, membrane injury, photosynthesis inhibition, simultaneously with an escalation in endogenous PAs, Pro, and boost up antioxidant enzyme activities in the roots of saffron (Duan *et al.* 2008).

### **Roles of signaling molecules in Salinity Tolerance**

**Nitric oxide:** Nitric oxide (NO) is a volatile gaseous signaling molecule, is concerned with the seed germination, growth and development, respiration, flowering, cell death, and stress response (Delledonne *et al.* 1998, Lamattina *et al.* 2003, Crawford 2006, Besson-Bard *et al.* 2008, Zhao *et al.* 2009). Bajgu (2014) recently demonstrated that NO inhibits lipid peroxidation by countering with lipid radicals and improves the action of antioxidant enzymes. Another important role of NO is related to regulation of plasma membrane H<sup>+</sup>-ATPase that creates an H<sup>+</sup> gradient, bestowing the force for Na<sup>+</sup>/H<sup>+</sup> exchange which influences K<sup>+</sup> and Na<sup>+</sup> homeostasis (Crawford 2006, Zhang *et al.* 2006a). Supplementation of exogenous of NO plays a significant roles in stress alleviation (Hossain *et al.* 2010, Sung & Hong 2010, Xiong *et al.* 2010) that have been associated to improved antioxidant activities, repression of lipid peroxidation (Zhao *et al.* 2004) and modulation of ROS detoxification system (Mishra *et al.* 2011).

**Hydrogen peroxide:** Earlier hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) is considered as ROS which is unwanted but unavoidable by-product under stress. But a recent study by Rhee (2006) has publicized its crucial role as redox signaling molecule in maintaining of normal growth and developmental processes, comprising with oxidative stress and therefore it has been well-known as an indispensable evil for cell signaling. H<sub>2</sub>O<sub>2</sub> functions in stress signals transduction (Hung *et al.* 2005, Hernandez *et al.* 2009) and association within H<sub>2</sub>O<sub>2</sub> and signaling networks has been significantly recognized for numerous stress responses (Larkindale & Knight 2002, Apel & Hirt 2004, Cheeseman 2007). Exogenous application of H<sub>2</sub>O<sub>2</sub> improves the membrane properties and minimum altered in ion leakage pattern in compared to controls. Recent studies have revealed that pre-treatment with exogenous H<sub>2</sub>O<sub>2</sub> counteract abiotic stress by maintaining leaf water relations, reducing peroxidation of membrane lipids, increasing stomatal conductance (gs) thus photosynthetic efficiency and improving the activities of antioxidant enzymes (Azevedo Neto *et al.* 2005, Wahid *et al.* 2007). In addition, it is believed that H<sub>2</sub>O<sub>2</sub> pre-treatment reduces Na<sup>+</sup> and Cl<sup>-</sup> content accrued by salinity and maintains greater tissue K<sup>+</sup> and Ca<sup>2+</sup> thus develops higher K<sup>+</sup>/Na<sup>+</sup> ratio. However further research are required for better understanding about this field.

### **Hormone regulation of salinity tolerance**

**Abscisic acid:** Abscisic acid (ABA) is one of the most essential phytohormone that plays a significant roles in many physiological processes associated with germination, growth and development, regulation of stomatal movement, biosynthesis of storage proteins and lipids and leaf senescence (Tuteja 2007). Besides, one of the major functions of ABA is in response to various abiotic stresses, stress signaling and osmotic stress tolerance. Upon subject to salt stress, plants show a proportional rise in ABA concentration due to water deficiency rather than ionic toxicity (Zhang *et al.* 2006b). A several studies demonstrated that synthesis of endogenous ABA in root xylem is associated with decrease leaves conductance after transported to leaves thus restricts of leaf growth (Jaschke *et al.* 1997, Cramer & Quarrie 2002, Cabot *et al.* 2009, Atkinson & Urwin 2012, Babu *et al.* 2012). On the other hand, ABA functions as a cellular signal that regulates the expression of a number of salt and water deficit-responsive genes. The biosynthesis and/or accumulation of ABA mitigates the negative effect of salinity on photosynthesis, assimilates translocation and thus growth (Popova *et al.* 1995, Jaschke *et al.* 1997). Gurmani *et al.* (2011) reported that the supplementation of ABA to *Oryza sativa* cv. IR-6 (rice) has an important role in alleviating salinity stress. ABA in roots assists to decrease Na<sup>+</sup> and Cl<sup>-</sup> ion concentrations by accumulating in vacuoles, increase K<sup>+</sup> and Ca<sup>2+</sup>, Pro accumulation and soluble sugar content which is crucial for adaptation under salinized environment (Jaschke *et al.* 1997, Chen *et al.* 2001, Gurmani *et al.* 2011). ABA also plays an important role in improving of xylem water potential as well as water uptake to the plant during salinity (Fricke *et al.* 2004).

**Indole Acetic Acid:** Besides functioning in various physiological and biochemical processes, indole acetic acid (IAA) also helps in decreasing salt-mediated injuries though there are very few reports regarding this event. Gulnaz *et al.* (1999) demonstrated that, salt-induced reduction in wheat seed germination is recovered by IAA treatment. Later on Akhiyarova *et al.* (2005) stated that IAA assists in formation of an attraction signal in the growth zone of leaf in response to saline stress. Exogenous application of auxin has been found to increase in plant morphological attributes in salt-stressed plant (Akbari *et al.* 2007). Foliar application with IAA counteracted the salt-induced negative effects by increasing essential inorganic nutrients accumulation and maintaining membrane permeability (Kaya *et al.* 2009). Kaya *et al.* (2009) also demonstrated an increase in chlorophyll, RWC content and decrease Na<sup>+</sup> concentration, electrolyte leakage while treated with exogenous IAA.

**Gibberellic acids:** Gibberellic acids (GAs) play an important role in seed germination, leaf expansion, stem elongation and flowering (Magome *et al.* 2004, Kim & Park 2008) thus in growth and development of plants. Besides their crucial use in several physiological and biochemical processes, they are well-recognized phytohormones in alleviating salinity (Kaya *et al.* 2009). Salt stress impairs the seed germination processes and reduces the growth and grain yield of wheat which is progressed by application of GA<sub>3</sub> (Kumar & Singh 1996). Exogenous application of GA<sub>3</sub> is reported to decrease the inhibitory effect of salt stress on growth traits, increase in photosynthetic pigments, RWC and enzymatic activity (Ali *et al.* 2011). Hamayun *et al.* (2010) observed the positive effect of exogenous GA<sub>3</sub> on salt-stressed soybean plant by boosting up the level of phytohormones, growth and development. Recent studies have shown exogenous application of GA<sub>3</sub> lessened the negative effects of NaCl-induced salinity by enhancing RWC, Chl content and counteracting the electrolyte leakage (Ahmad *et al.* 2009), regulating the ions uptake, ion partitioning and hormones homeostasis (Iqbal & Ashraf 2013), lowering stomatal resistance and increasing plant water relationships (Maggio *et al.* 2010). Lipid peroxidation is indispensable in salt stress counteracting by application of GA<sub>3</sub> thus shows improve resistance to salinity (Ahmad *et al.* 2009).

**Jasmonic acid:** Jasmonic acid (JA) and its methyl esters are crucial cellular regulators included in varied physiological and developmental processes, like germination, root growth, fertility, stomatal regulation, fruit ripening and senescence (Wasternack & Hause 2002, Cheong & Choi 2003, Hossain *et al.* 2011b). Rohwer & Erwin (2008) stated the positive role of JA in plant responses to abiotic stresses; however, the role of most of the derivatives of JA is still unclear. There are little reports on the function of exogenous JA in plant response to NaCl salt stress. JA pre-treatments assist in the synthesis of abundant proteins (Known as JIPs) in response to abiotic stress alleviation and/or tolerance (Sembdner & Parthier 1993). MeJA (methylated ester of JA) supports protection in stress by osmoregulation and enhanced Pro accumulation (Fedina & Tsonev 1997). Exogenous application of JA on salt treated plants regulates the balance of endogenous hormones such as ABA (Kang *et al.* 2005), GAs (Seo *et al.* 2005) which grant significant protection mechanisms under salinized environment.

**Salicylic acid:** Salicylic acid (SA) is a plant-derived phenolic compound that performs a significant role in plant growth and development along with the response to abiotic stresses (El-Tayeb 2005, Ahmad *et al.* 2011, Fragnière *et al.* 2011, Tahjib-Ul-Arif *et al.* 2018). El-Tayeb (2005) found increased synthesis of Chl and carotene (Car), and maintained membrane integrity to barley with SA pre-treatment leading to the development of plant growth. Several studies have demonstrated that SA improves salinity tolerance by restoring membrane potential and checking salt-induced K<sup>+</sup> loss (Jayakannan *et al.* 2013), accumulating of K<sup>+</sup>, and soluble sugars in roots (El-Tayeb 2005). SA treatment showed improved growth, lessened lipid peroxidation and membrane permeability in maize (Gunes *et al.* 2007), minimized leaf Na<sup>+</sup>, Cl<sup>-</sup>, and H<sub>2</sub>O<sub>2</sub> content with increased photosynthesis in mungbean (Nazar *et al.* 2011) and Intil (Stevens *et al.* 2006, Poór *et al.* 2011), enhanced grain yield in wheat (Arfan *et al.* 2007) under salinized condition. SA application triggers the accumulation of ABA and IAA, assists in the development of anti-stress programs in wheat seedlings thus, accelerates growth and developmental processes (Sakhabutdinova *et al.* 2003). Gémes *et al.* (2011) reported SA-induced generation of H<sub>2</sub>O<sub>2</sub> and NO are believed to assist in cross-tolerance to various stressors. Exogenous application of SA decreased the NaCl-induced electrolyte leakage and showed adaptive responses in alfalfa plant under salt stress (Torabian 2011). Moreover, Yusuf *et al.* (2012) observed SA induced antioxidant activities (SOD, CAT and POX) in mustard which might be accountable for improved tolerance of mustard to NaCl stress.

**Brassinosteroids:** Brassinosteroids (BRs) is one of the most recent groups of phytohormones act as a strong growth inducer and stress response aid (Anuradha & Rao 2001, Krishna 2003, Ashraf *et al.* 2010, El-Mashad & Mohamed 2012). Anuradha & Rao (2001) reported that BRs plays an important role in activation of seedling growth and development (Clouse & Sasse 1998) under salt stress which was related with increased levels of nucleic acids and soluble proteins. Several studies have revealed the prospective application of BRs in agriculture to improve yield and regulate crop growth under stress (Houimli *et al.* 2010, Hayat & Ahmad 2011, El-Mashad & Mohamed 2012). Exogenous BR application increases the fresh and dry weight of plant (Houimli *et al.* 2010), enhances plant biomass in wheat (Shahbaz & Ashraf 2007), and alleviates the injurious effect on nuclei and chloroplasts (Krishna 2003). Foliar application of BRs assist to overcome the adverse effect of salinity on photosynthetic pigments, crop productivity thus increased yield attributes in wheat (Eleiwa *et al.* 2011), increase the concentration and total uptake of nutrients (N, P, K,

Fe, Mn, Zn and Cu) in straw and grains (Eleiwa & Ibrahim 2011). Later on, El-Mashad & Mohamed (2012) demonstrated that foliar spray of BR (0.05 ppm) alleviated salt stress by b activities of enzymatic and non-enzymatic antioxidants.

#### ***Application of macromolecules in salt stress tolerance***

In the recent era scientist have been showing much interest to demonstrate the positive role of Ca in alleviating the adverse effect of NaCl-induced salt stress (Roy *et al.* 2019). Application of Ca plays a part in the regulatory mechanisms that activate the plants adapt to adverse salinized condition by improving RWC plants. Ca treatment increases the photosynthetic capacity by rehabilitating the photosynthetic pigments, reduces the oxidative damage through regulating the antioxidant defense mechanism and Pro biosynthesis (Parvin *et al.* 2015, Roy *et al.* 2019).

#### ***Trace elements in salt stress mitigation***

**Selenium:** During the last two decades several studies documented the positive effect of selenium (Se) on plant growth, development and productivity at low concentrations (Turakainen *et al.* 2004, Hasanuzzaman & Fujita 2012a, Hasanuzzaman *et al.* 2012b) alone with resistance to certain abiotic stresses (Cartes *et al.* 2010, Chu *et al.* 2010, Djanaguiraman *et al.* 2010, Hasanuzzaman *et al.* 2010b). Exogenous application of Se counteract the inimical effect of salt stress by regulating the SOD and POD activity when applied to a concentrations ranging 1–5 mM (Terry *et al.* 2000), enhancing Pro content (Djanaguiraman *et al.* 2005), reducing NaCl-induced lipid peroxidation (Walaal *et al.* 2010).

**Silicon:** A few evidences have been documented about the positive role of silicon (Si) to counteract the salt stress. Kim *et al.* (2014) Showed that (Si) application to rice root zone prompted the hormonal and antioxidant responses thus significantly increased rice plant growth under salinity stress.

### **CONCLUSIONS**

Based on a profuse research findings, it is obvious that salt stress has detrimental effects on the physiological and biochemical processes associated with growth, development, the yield of plants. Counteracting the negative effect of salinity involves a complex of responses at the cellular, molecular, metabolic, physiological as well as whole plant levels. Plentiful research on cellular, metabolic and physiological strategies regulation demonstrated the positive role against salt stress tolerance and/or adaptation by controlling ion uptake, transport and balance, improving osmotic regulation, hormone metabolism, antioxidant enzymatic activity, and stress signaling. Further experiments are needed to launch for better understanding of the underlying mechanisms in salt stress mitigation.

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