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Varied Responses and Tolerant Mechanisms towards Salinity Stress in Plants

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Author's contribution

The sole author designed, analyzed and interpreted and prepared the manuscript.

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ABSTRACT

Among several abiotic stresses, which retard crop production on at least 1/5th of irrigated land worldwide, high saline conditions seems to be the most severe environmental stress. The plant can reveal the effects of salinity at any of its life cycle stage *viz.* germination, seedling, vegetative or maturity. However, the response can vary for different plants on a given salt concentration and consists of numerous morphological, physiological, biochemical and molecular changes which function in a well coordinated way to alleviate toxicity.

The reduction in growth and yield of crop plant may be attributed to the production of Reactive Oxygen Species (ROS), nutrient ion and osmotic imbalance, ion toxicity which is due to the accumulation of Na^+ and Cl^- ions under continuous exposure of plant to saline conditions. Moreover, varied biochemical phenomenon *viz.* change in proteins, enzymes expression level, chlorophyll and amino acids content etc. can also be observed in these crops. However, the plants may evade themselves with three different mechanisms i.e. osmotic stress tolerance, Na^+ or Cl^- exclusion, and by means of tissue tolerance to sodium and chloride ions. Under high salinity stress, products of enhanced activities of multiple genes encode osmolytes, ion channels, receptors, components of calcium signaling, and some other regulatory signaling factors or enzymes which enable the plant then to tolerate high salinity stress.

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1. INTRODUCTION

As compared to exponential growth of human population, which is expected to reach 9.3 billion by the year 2050, the crop production is increasing arithmetically. The ultimate result is decreasing ratio of crop production year by year (httl://www.unfpa.org/swp/200/). Number of environmental factors contributing for their negative impact on productivity are stresses such as high and low temperature, drought, alkalinity, salinity, UV stress and pathogen infection. Among these factors, salinity is the major one that negatively affects plant productivity by impairing crop production. Approximately, 7% of the world's land area, 20% of the world's cultivated land and nearly half of the irrigated land is affected with high salt contents [1,2]. According to [3], 20% of irrigated land worldwide (Fig.1) has been affected with salinity which poses a severe threat for the cultivation of crops in arid and semiarid agricultural lands. India has 8.6 M ha salt affected area out of which 3.4 M ha is under sodicity and rest under salinity.

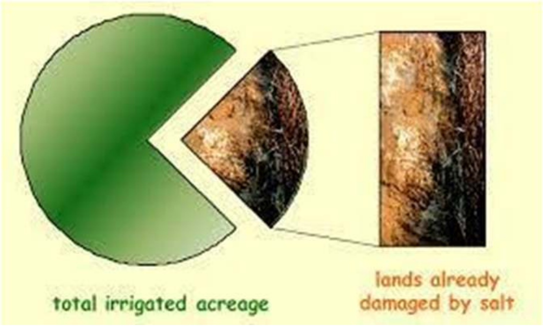

Fig. 1. Percentage of irrigated lands damaged by salinity

The forces mainly seem to contribute for salinization processes are capillary water level elevation and subsequent evaporation of saline groundwater. The release of various soluble salts like sodium, calcium, and magnesium by weathering of rocks into the soil is other natural cause of salinity. Irrigating the field with the salt water, where the drainage is poorly present, is the most serious factor causing salinization and resulted in the loss of once productive agricultural land. After evaporating, the water leaves behind the salts of calcium and magnesium carbonates, leaving Na^+ dominant in the soil [4,5]. This dominance of sodium ions further results into the reduction of the concentration of macronutrients as well as micronutrients by the one or two order of magnitude respectively; however, it may be even more in later. The arid regions are more susceptible to salinization in this context .Another anthropogenic activity - the use of ice melters on roads and sidewalks - where the landscape soil comes from is important source of salt. This addition of any soluble material will enhance soil salinity [6]. Whereas many crop species are very sensitive to soil salinity, some are the salt tolerant. The former are known as glycophytes and later as halophytes. In general, glycophytes cannot grow even at moderate salinity level of 100 mM NaCl, halophytic plants, on other hand, can grow at salinities over 250 mM NaCl because of their ability to exclude Na^+ and Cl^- by roots while water is taken up from the soil. Halophytic plants also possess the ability to prevent the building-up of salt in the cytosol by sequestering and accumulating it in vacuoles. In contrast, the salt sensitive crops generally cope up with salt stress by restricting the uptake of salts and by synthesizing various compatible solutes like sugars, amino acids etc. to maintain osmotic equilibrium. Since, halophytes offer a possibility of using them as alternative crop, an understanding of their physiology of salt tolerance might help in increasing salt resistance in the existing crop plants. In this review, attempt has been made to describe the adverse effect of salinity stress and the general mechanism for the stress tolerance in plants.

2. SALINITY EFFECTS

A soil is classified to be saline if its electrical conductivity (EC) is more than 4 dSm^{-1} (40 mM NaCl) which can be determined mainly by the presence of sodium cations along with usually soluble anions, chloride and sulphate, in soil. However, very mild or no effect on plant yield could be seen at low salt concentration. But with increase in concentrations, most crop plants (glycophytes) exhibit decrease in yield almost zero and severely affected or even killed at salt concentration of 100-200 mM NaCl. Various physiological and biochemical processes are affected under saline conditions which result in reduced biomass production. The adverse effects of salinity can be seen at almost all the growth stages of plants *viz.* germination, seedling, vegetative and reproductive stages. The deleterious effects of salinity can be noticed in terms of low osmotic potential of soil solution (water stress), reduction in uptake of K^+, NO^- PO_4^{3-} etc. due to high level of Na^+ and Cl^-, ion toxicity or combination of these factors [7]. During the onset and development of salt stress within a plant, all the major processes such as carbohydrate metabolism, protein synthesis and lipid metabolisms are affected. High salt levels lead to damaging effects on plants as well as increase the pH-level of soil on which most crop plants are not able to grow. Alteration in soil structure and microenvironment of soil (i.e. air-water balance) essential for biological processes occurring at plant roots has also been reported. Soils with high salt concentration are known to cause reduction in growth and yield of different crops [8-10]. This reduction in growth and productivity is explained as resulting from decrease in the photosynthetic activity which in turn is attributed to the reduced chlorophyll content [11,12]. Depending on the type of salts present, there may be issue of suppression of uptake of particular nutrients by plant through ionic competition (an ion is an electrically-charged particle, and is the form that nutrients and toxins are taken up by plants). In case, there is large amount of one nutrient/toxin, it will be more likely to be taken up than others. A number of salt ions are known to produce their potential effects on plants as follows:

Chloride – competes with anions for uptake, particularly nitrate. Chloride toxicity symptoms include early leaf drop and leaf “burn” or drying of leaves (usually, the *tips* of older leaves are affected before other plant parts).

Sodium – competes with cations for uptake, particularly potassium. Sodium toxicity symptoms include leaf “burn” or drying of leaves (usually, the *margins* of older leaves are affected first).

Potassium – competes with cations for uptake, particularly calcium and magnesium; plant uptake of nitrogen can be suppressed if potassium levels are excessive. Potassium ions are one of the essential elements required for growth. Alterations in K^+ ions uptake (because of the high Na^+ concentration in soil due to salinity stress) can disturb the osmotic balance, stomatal functioning and enzymes activities.

Sulphate – competes with anions for uptake, but sulphur toxicity is extremely rare.

The different crop types may have varied salinity tolerance; some will readily grow in soils that more sensitive plants would not grow at all. For example, squash and zucchini tolerate much higher salt levels than potatoes or strawberries, and grain crops are more tolerant of salts than fruit and vegetable crops. Further, at given concentration of salinity, these grain crops respond differently. Whereas, rice plants die at salinity level of 10 dSm^{-1}, wheat shows only reduction in yield. Barley, on the other hand, is mildly affected at the same salinity level**.** This varying tolerance level of plants against salinity depends upon species, the phenological stage of the plant and the salinity level to which plant is exposed.

2.1 Morphological and Physiological Changes under Salinity Stress

It is known that salinity affects many aspects of plant metabolism and induces changes in the morphology of plants. These changes are considered either the adaptations increasing stress endurance of plants imposed by salinity or the signs of damage and disruption of normal equilibrium of life processes. A number of workers, in past and recent, have carried out their work on different crops to evaluate the effects of various salinity levels at different stages of plant development. Earlier studies have reported a number of morphological and anatomical changes in halophytes in response to salinity stress. These included stunting growth, increase of succulence, earlier occurrence of lignification, change in number and size of stomata etc. [13,14]. Development processes such as seed germination, seedling growth and vigour, vegetative growth, flowering and fruit set could also be visualized under high saline conditions [15]. It has also been reported that several aspects of reproductive growth including flowering, pollination, fruit development, yield and quality are also influenced by salinity [16]. While working on maize, [17] have shown the effect of different NaCl concentrations on root and shoot fresh weight, root & shoot length and number of leaves. It was concluded in their study that at 100 mM NaCl concentration, the maize revealed maximum decrease in its fresh weight and length of root and shoot; however, at 50 mM NaCl, there was observed maximum increase in root and shoot length in maize as compared to control. On the other hand, in cotton, it is the concentration of 200 mM which had profound effect on plant height, biomass and seed germination [18]. Similarly, such inhibition in root and in particular Shoot growth was observed with NaCl treatments for sugar beet, rice and cotton seedlings at higher salt treatment i.e.200 mM [19]. Another effect of higher salinity on the reduction of leaf area and leaves number has also been observed in number of plants viz. *Aloe vera* L., *Capsicum frutescens* L., *Zea mays* L. and *Sorghum bicolor* L. [17,20-22]. Under salinity stress, plant growth was found to be inhibited due to different phenomenon *viz.* the low water potential, ion toxicity and imbalance excreted by salinity [23]; this was further supported by experimental work carried on sprout, peanut, soybean and savory [24-27]. Further, the degree of growth inhibition due to osmotic stress depends on the time scale of the response for the particular tissue and species in question, and whether the stress treatments are imposed abruptly or slowly [7,28].

As morphological changes in response to saline stress are not enough to determine its effects, it becomes important to study other physiological and biochemical responses in plants to better understand the effect of salinity stress. The exogenous application of salt is well known to cause water deficit, ion toxicity and water stress. However, the recent work on rice has shown that the salinity induced changes in plants are ionic rather than osmotic [29]. The most important physiological process affected under high saline concentration is photosynthesis. By reducing water potential, salt stress inhibits photosynthesis in plant which in turn attributed to closure of stomata as studied in *Cucumis* [30]. The facultative halophytic plants such as *M. crystallinum,* to tolerate salt stress conditions, were shown to shift their C3 mode of photosynthesis to CAM. It may help in preventing the loss of water by opening stomata at night [31]. Moreover, salt-tolerant plant species such as *Atriplex lentiformis* revealed a shift from C3 to C4 pathway in response to salinity [32]. Electron microscopic studies in plants like potato and *Eucalyptus*, after giving treatment with NaCl, have shown the disorganized structure of chloroplasts which included distortion of the thylakoidal structure due to its swelling and increase in the size and number of plastoglobuli; however, the starch content was found to be decreasing with larger starch grains [32]. Apart from the above mentioned changes, a number of other processes associated with photosynthesis *viz.* decrease in the photosystem II efficiency, and electron-transport chain (ETC), and decreased CO_2 assimilation rate are also influenced under high salinity conditions [33].

Besides decreasing photosynthetic rate in plants, effects of salt stress on membrane instability resulting from calcium and potassium displacement by sodium, and membrane permeability have also been studied [34,35]. The control of transport of salt across the membrane seems to be fundamental basis of adaptation towards salinity stress. So, the primary site where the effect of salinity can be seen is the plasma membrane and the tonoplast. The salt sensitive cultivars were always shown to have greater increase in cell membrane permeability as compared to salt tolerant cultivars. The comparative studies between salt tolerant and salt sensitive plants have indicated the tolerant feature of former due to greater plasma-membrane integrity because of more lipids and proteins sustainability, and lower peroxidative and oxidative alterations in lipid and protein molecules respectively as compared to salt sensitive cultivars [36-38]. Calcium is also known to play an important role in cell membrane stabilization and hence, the displacement of ca^{+2} from its binding site ma y results in plasma-membrane instability and also salt tolerance. It has been reported that resistance to salt is correlated negatively with Na^+ concentration and positively with K^+ concentration. Also, high K^+/Na^+ in plant tissues, has been considered as an important physiological solution for salinity tolerance [39,40]. Overloaded sodium ions around the root exterior disturb uptake of potassium. Shortage of potassium inside the cell unavoidably leads to decrease in plant growth, as K^+ is the most abundant cellular cation which plays an important role in preserving membrane potential, enzyme activities and cell turgor [41].

2.2 Biochemical Indicators under Salinity Stress

The mechanism in plants to cope up with adverse conditions of salt stress involves either accumulating high concentrations of inorganic ions or low molecular weight organic solutes. These ions or solutes play an important role in higher plants. However, their relative contribution varies among species, cultivars, and even between different compartments within the same plant [42]. A brief detail of these is given below:

2.2.1 Soluble sugars

Generally, the accumulation of different kind of sugars in plants under saline conditions is carried out for the maintenance of osmoregulation in plants. Osmoregulation by definition is the adjustment of the osmotic pressure of a cell or an organism in relation to surrounding fluids. In glycophytes, sugars contribute up to 50% of the total osmotic potential under saline conditions [43]. However, the recent study on rice [44] showed the higher accumulation of total soluble sugars, essential for osmotic adjustment, in shoots of salt-tolerant plants as compared to sensitive-ones. The soluble sugars accumulating under saline conditions can be of different types. The occurrence of these varied types of carbohydrates such as sugars (glucose, fructose, sucrose, fructans) and starch in plants under salt stress has been reported [45]. Their roles have also been clearly defined in osmoprotection, osmotic adjustment, carbon storage, and radical scavenging. Similarly, another kind of disaccharide sugar, Trehalose, was found to be accumulating in many organisms under various abiotic stresses and also reported to be both an osmolyte and an osmoprotectant [46].

2.2.2 Proteins

Besides above mentioned sugars, the potential of good number of proteins imparting tolerance against salinity has also been shown in different crops [47,48] which revealed that salinity promoted the synthesis of salts stress-specific proteins. Depending upon the plant species an increase or decrease in the total content of proteins could be observed under varying salinity levels. These may be synthesized *de novo* in response salt stress or may be present constitutively at low concentration and increase when plants are exposed to salt stress [49-50]. The proteins accumulating under salt conditions serve the purpose of storing nitrogen that can be utilized by plant later on and can play a role in osmotic adjustment [47]. A higher content of these soluble proteins has been observed in number of salt tolerant cultivars like barley, sunflower, finger millet, and rice [51]. Contrary to that, a significant decrease in protein content was recognized in sugar beet and tomato, as compared with control, in response to salinity stress [52-54]. This decrease in soluble protein could be explained on the basis that higher salinity may induce degradation of nuclear RNA and this reduced RNA content further affects the protein synthesis. Further, the appearance of high proline concentration under salt stress may be due to more protein breakdown to face the adverse conditions of salinity stress.

2.2.3 Amino acids

The accumulation of protein amino acids (alanine, arginine, glycine, leucine, and valine), together with the imino acid (proline) and the non-protein amino acids (citrulline and ornithine) and amides (glutamine and asparagines) have been reported in plants facing salt stress. The accumulation of widely occurring stress protein – proline- is generally taken as well known criteria for measuring alleviation of salinity stress and drought tolerance. However, in rice plants grown under salt stress, the appearance of proline at early stages has been shown as the result of salt injury, not as an indication of salt tolerance [55]. Substantial contribution of proline towards the cytoplasmic osmotic adjustment, membrane stability and mitigating the effect of NaCl on cell membrane disruption besides regulating the accumulation of useable nitrogen has clearly been explained by different workers [56-58]. Another important role of proline in improving salt tolerance in *Nicotiana tobaccum* has also been reported where proline accumulation resulted in increase of the enzymes activities involved in antioxidant defence system of this plant [59]. In contrast to above studies, it has observed that an increase of proline content in *Simmondsia chinensis* (Link) Schneider (jojoba plant), after salinity application, is a physiological response of plants rather than biochemical under salt stress [60].

2.2.4 Polyamines and polyols

Polyamines play an important role in normal growth and development in plants. These are the amino groups containing polyvalent compounds. Whereas putrescine, spermidine and spermine are the most commonly occurring polyamines in higher plants, diamines, diaminopropane and cadaverine occur less commonly [56]. On the basis of their biological role, these have been classified into two groups, first group includes putrescine and cadaverine, the second contains spermidine and spermine. Like auxins and gibberellins plant hormones, putrescine and cadaverine, belonging to former group of polyamines, play an important role in cell elongation and root formation [61]. The latter group containing spermidine and spermine controls cell division, organogenesis, and plant senescence like cytokinins [62,63]. Apart from playing their role like hormones, these polyamines also contribute in stabilizing the macromolecules *viz.* DNA, RNA and phospholipids in the cell at pH 7. This hydronium ion concentration makes frequent binding of polycationic polyamines to the polyanions mentioned above.

On the other hand, polyols are the polyhydric alcohols are involved in osmoregulation and playing a role in plant salt tolerance [64]. Polyols are found in plants in two forms - acyclic form which includes mannitol, glycerol, sorbitol, and cyclic form includes ononitol and pinitol. In general, their occurrence in cytoplasm of some halophytes is considered as the result to overcome the osmotic disturbances caused by high concentrations of inorganic ions compartmentalized in vacuoles. These polyols function either as an enzyme stabilizer or maintaining the membrane structures that are sensitive to dehydration or ionically induced damage.

2.2.5 Antioxidant

Exposure of plants to salinity stress leads to the generation of free radical species or Reactive Oxygen Species (ROS) like H_2O_2 (hydrogen peroxide), O^{2-} (superoxide) and .OH (hydroxyl radical) which cause damage to metabolic processes and lead to senescence and eventually cell death. To defend against these free radicals, plants have evolved a mechanism of scavenging ROS by inducing certain antioxidative enzymes such as catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR), and superoxide dismutase (SOD) [65]. The induction of certain non-enzymatic antioxidants *viz.* vitamin C, vitamin E, carotenoids and others in the protection against oxidative stress has also been reported (66). A positive correlation between salinity tolerance and the activity of these antioxidant enzymes with the accumulation of non-enzymatic antioxidant compounds has been studied [67].

3. MOLECULAR RESPONSES TOWARDS SALINITY

Salt tolerance appears to be due to combination of genes that contribute to salt and osmotic regulation in different parts of the cell and the plant. A number of evidences have shown that the susceptibility or tolerance to high salinity stress in plants is a coordinated action of multiple stress responsive genes. These genes can be induced early or late under saline conditions. Induction of early responsive genes takes place within minute after perceiving salt exposure which in turns activates delayed responsive genes to face harsh conditions of salinity. The halophyte *Mesembryanthemum crystallinum* and glycophyte *Arabidopsis thaliana* have emerged as a model system for understanding the molecular response to salt-stress [68,69], and substantial data is now available on the genes expressing under saline conditions in different crops [70-73]. Further, the expression of these genes was found to be dependent on type of tissue, developmental stage of plant and the extent to which salinity stress is given to plants [14,74-76]. As salt response is a quantitative trait, the information about the expression levels of a large number of genes simultaneously based upon micro- and macroarray-based transcriptional profiling has been shown in *Arabidopsis* and rice [74,77-78]. Mutation studies in *Arabidopsis* have helped in the identification of key genes (*sos1*-*sos4*) in salinity tolerance [77]. These genes were found to encode different proteins which respond differently under different salt stress conditions. Based on microarray analysis, 57 and 43 genes induced by salinity and ABA respectively were also identified in rice [78]. Similarly, the upregulation of genes *viz. GST* and *APX* involved in defence against ROS were found in rice plants 24 hrs after stress imposition [74]. Besides *Arabidopsis* and rice, other organisms like *Escherichia coli* and *Saccharomyces cerevisiae* (yeast) have also been employed to identify salt responsive genes [79]. However, in yeast and plants, ion homeostasis under salt stress has received much attention. Processes important for ion homeostasis include cellular uptake, sequestration and export and long-distance transport. Various ATPases, water channel proteins and ion transporters are regulated by salt stress either at the mRNA or protein levels as suggested by previous gene regulation studies. *AtNHX1* was the first plant Na+/H+antiporter gene to be characterized functionally. It was found to encode a tonoplast antiporter homologous to the yeast Na+/H+ antiporter Nhx1 [80]. The over–expression of *AtNHX1* conferred salt tolerance to transgenic *Arabidopsis* plants was demonstrated by [81]. A large number of genes and proteins, such as HKT and NHX, encoding K^+ transporters and channels have been identified and cloned in various plant species. It has also been shown that tonoplast-localized NHX proteins (NHX1 and NHX2) are essential for active K^+ uptake at the tonoplast for turgor regulation, and for stomatal function [82]. In fact more such NHX isoforms have been identified and their roles in ion (Na^+, K^+, H^+) homeostasis established from different plant species [83].

The transcriptome analysis of gene expression at the mRNA level has greatly contributed to our understanding of abiotic stress responses. The study of tobacco leaf apoplast proteome identified 20 proteins whose expression changed in response to salt stress. These included stress associated proteins, together with chitinases, germin-like proteins and lipid transfer proteins [84]. Recently, transcriptome analysis of chickpea genotypes (salt tolerant and salt sensitive) has been carried out to investigate the responses of genes at different developmental stages of plants [85]. Their reports have revealed the appearance of 19% of novel gene loci in the root transcriptome when analysed under salt stress conditions. Further, the gene encoding enzymes involved in biosynthesis of amino acids (proline & citrulline), polyamines and sugar alcohol (inositol and trehalose) were found to be up-regulated under stress conditions.

4. SALINITY TOLERANCE MECHANISMS

The crop plants under salt stress conditions either try to escape themselves by avoiding the stress or employing the different mechanisms to acclimatize to salinity. However, with different responses by a plant when grown under different saline conditions, the mechanism of salinity tolerance becomes even more complicated. The three types of plant response (Fig. 2) as described [86] are a) the tolerance to osmotic stress, b) the Na^+ exclusion from leaf blades and c) tissue tolerance:

4.1 Osmotic Stress Tolerance

Osmotic stress is a condition in which solute concentration in water changes suddenly which may further affects its movement across the cell membrane. Plants start experience water stress during early stages of exposure to salinity. One important response to osmotic/water stress is the accumulation of the abscisic acid (ABA) – a plant hormone, which induces several responses to osmotic stress. This results in reduced cell expansion in root tips and young leaves and stomatal closure which finally affect evaporation rate and overall water transport [87,88]. For a moderate salinity stress, an inhibition of lateral shoot development becomes apparent over weeks, and over months, there are effects on reproductive development, such as early flowering or a reduced number of florets. During this time, a number of older leaves may die; however, production of younger leaves continues. All these changes in plant growth are responses to the osmotic effect of the salt, and are similar to drought responses.

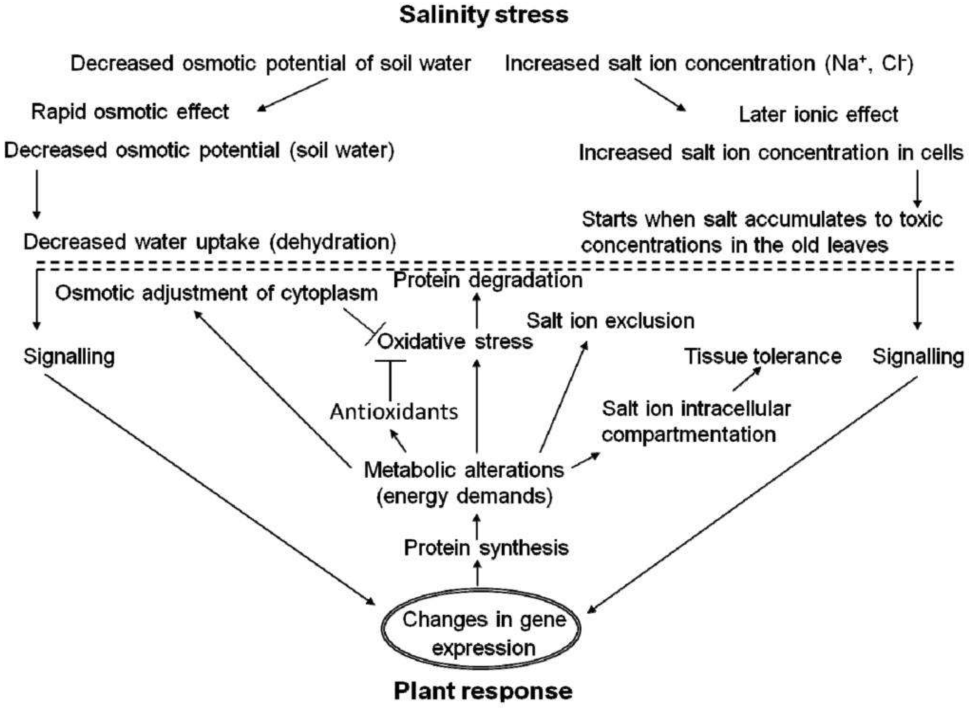

Fig. 2. Different types of plant responses under salinity stress

(Source; see reference [89])

4.2 Na^+ Exclusion

When a plant is grown under saline conditions, it is generally found that Na^+ concentration reaches at toxic level fastly as compared to Cl^- in majority of crop plants. So, it is always better to focus on a mechanism of Na^+ exclusion and control over its transport within the plant [86]. It can be achieved by mechanism that involves minimizing the accumulation of Na^+ in the cytosol of cells especially of transpiring leaves. Number of specific ion channels and transporters are involved in it for allowing the control of Na^+ transport throughout the plant [86,90]. Na^+ exclusion from leaves is inbuilt mechanism in cereal crops like rice, durum wheat, bread wheat and barley to provide tolerance against salinity [91]. One of the efficient ion channels reported in plants to drive potentially harmful ions from cytosol into large, internally acidic, vacuoles is vacuolar Na^+ /H^+ antiports. These ions help in decreasing osmotic potential within the vacuole so that water starts flowing into the cell and it helps plants to continue to grow in high saline soils. This downhill movement of H^+ (down its electrochemical potential) with uphill movement of Na^+ (against its electrochemical potential) by antiports involves the use of e.m.f generated by vacuolar enzymes like H+-ATPase and H+-PPiase which results in exclusion of Na^+ out of cytosol. The above mentioned mechanism should compensate for by the uptake of K^+. If not compensated, it will require a greater demand for organic solutes for osmotic adjustment by the plant. There are certain kinds of membrane receptors and membrane proteins /enzymes on plasma membrane which are sensitive for extracellular and intracellular Na^+ respectively. Among these various types of Na^+ sensor(s), the plasma-membrane Na+/H+ antiporter - Salt Overly Sensitive1 (SOS1) is a possible candidate [92]. In fact, the SOS signal pathway is mainly responsible for maintaining ion homeostasis in *Arabidopsis* [93]. Generally, the force to activate SOS pathway comes from high salinity (Na^+) stress which first initiates a calcium signal, then the pathway. Firstly, a calcium sensor – SOS3 sense the change in cytosolic Ca^{2+} ions and then it interacts with the SOS2 protein kinase. This SOS3-SOS2 protein kinase complex phosphorylates SOS1, resulting in outflow of excess Na^+ ions. In particular, SOS1, encoding a plasma membrane Na^+ /H^+ antiporter, plays a critical role in Na^+ extrusion and in controlling long-distance Na^+ transport from the root to shoot [94,95]. Both the protein kinase SOS2 and its associated calcium-sensor subunit SOS3 are required for the post-translational activation of SOS1 Na^+/H^+ exchange activity in *Arabidopsis* [96,97], and in rice [98].

4.3 Tissue Tolerance

The mechanism involves an increase of survival of old leaves by compartmentalizing Na^+ and Cl^- at the cellular and intracellular levels. It results in avoidance of piling up of their toxic concentrations within the cytoplasm of mesophyll cells in the leaf [86], and also the synthesis and accumulation of compatible solutes within the cytoplasm. The compatible solutes comprise not only nitrogen containing compounds such as amino acids, betains but also organic acids and sugars [56]. These solutes play a role in plant osmotolerance by the ways of protecting the enzymes from denaturation, stabilising membrane or macromolecules or playing adaptive roles in mediating osmotic adjustment [99]. The increase in proline and glycine betaine (GB) - the best known compatible solutes have been revealed under salt and drought stresses [100] and constitute the major metabolites found in durum wheat under salt stress, as in other members of Poaceae [101,102]. Proline, a proteinogenic amino acid, not only plays a role in stabilizing protein and membranes structures but also as osmolyte for osmotic adjustment and scavenging free radicals generated under stress conditions. GB being a amphoteric compound, apart from above mentioned role, also plays a role as a scavenger of ROS generated during various stresses viz. salt, cold and drought. However, while proline is probably the most widely distributed osmolyte accumulated in plants [103], the occurrence of GB seems to be restricted to several halophytes and a few crop plants [104]. The role of SA (Salicylic Acid) in improving salinity tolerance by restoring membrane potential and preventing salt-induced K^+ loss via a guard cell have recently shown in *Arabidopsis*.

5. CONCLUSION

The worldwide agriculture land now a days has been affected mainly by salinity which will prove to be a significant problem in near future. The detrimental effects of high salinity on plants can be observed at the whole-plant level in terms of plant death and/or decrease in productivity. However, some plant species are more tolerable than others in their survival in salty conditions. To understand clearly the mechanism of salinity tolerance and to develop the salinity tolerant lines/cultivars to cope with the salinity constraints, application of both the approaches of gene manipulation and traditional breeding will be required. Recently, a novel role of pea G-protein in high salinity stress tolerance has also been observed. However, in other crops, the role of G-proteins in salinity has not been well studied. The exploitation of salinity stress responsive genes of new pathways, including DNA/RNA metabolism and G-proteins signaling pathways, will be helpful for engineering salinity-tolerant crop plants.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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