

Plants and Salt stress

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ABSTRACT: Soil salinity is one of the major environmental problems affecting agricultural production in arid and semi-arid regions of the world, both in irrigated and dry land agriculture. The deleterious effects of salinity on plant growth are associated with low osmotic potential of soil solution causing physiological drought, nutritional imbalances and specific ion toxicity or combination of all these factors. Plant growth responds to salinity in two phases: osmotic phase that inhibits growth of young leaves and ionic phase that accelerates senescence of mature leaves. Plant adaptations to salt stress are of three diverse types: osmotic tolerance, sodium, chloride exclusion and the tolerance of tissue to accumulated sodium. Ability of plant cells to keep low cytosolic sodium concentrations is an essential process associated with the capacity of plants to grow in high salt concentrations. Traditional breeding programs trying to improve abiotic stress tolerance have had some success but are limited by the multigenic nature of the trait. Number of tolerant plants is reported in recent years such as *Mesembryanthemum crystallinum* and *Thellungiella halophila*. *Arabidopsis thaliana* is a genetic model plant, and widely used for unravelling the molecular basis of stress tolerance. Molecular genetics and functional genomics provide a new way to synthesize molecular and physiological knowledge to improve the salinity tolerance of plants. The aim of this review is to provide a basic biological understanding of salt stress and plant responses.

Key Words: salt stress, plants, QTL, salt tolerance

INTRODUCTION

Abiotic stress causes a decline in crop growth and productivity. Salt stress causes loss of water use efficacy, increase ions, induction of heat stress and reduces stem extension. Biological macromolecules are damaged due to production of free ions (Farooq *et al.*, 2009). It was found that salinity stress resulted in decrease of water content, accumulation of hydrogen peroxide and electrolyte release in plants (Mandhania *et al.*, 2006). One of the severe factors is salt accumulation in soil limiting the productivity of plants, causes adverse effects on germination, plant growth and crop yield (Munns & Tester, 2008). Throughout world, about 45 million hectares of irrigated land affected by salt (Munns and Tester, 2008). Salt stress affects plants in numerous ways such as; ion toxicity, nutritional disorders, physiological drought, oxidative stress, modification of metabolic processes, membrane incompetence and reduction of cell division (Zhu, 2007).

High salt concentration reduces plant growth, development and survival. When Plant exposed to high salt concentration all the major processes are affected (Parida and Das, 2005). When plant exposed to high salt at germination it causes physiological drought and reduction in leaf expansion. The osmotic effects of salinity stress can be observed immediately after salt application and are believed to continue for the duration of exposure, resulting in inhibited cell expansion and cell division, as well as stomatal closure (Munns, 2002). If plant exposed for long time to to salinity, plants face ionic stress, which can direct to premature senescence of adult leaves, and thus a reduction in the photosynthetic area available to support continued growth (Cramer and Nowak, 1992). High sodium, chloride concentration has the ability to affect plant enzymes and physiological processes. Premature senescence, chlorosis, necrosis in leaves due to high Na^+ which affects plants by disrupting protein synthesis (Munns, 2002,). Plants have several salt tolerance mechanisms. Plants may eliminate salt from their cells and may tolerate its presence within the cells. In this review paper, our focus to discuss about high salt, effects of salt on plants and tolerance mechanisms. These tolerance mechanisms help plants to withstand stress.

Salt Stress

Today plants facing a variety of biotic and abiotic stresses in changing environmental conditions. Salinity is a severe problem for temperate and tropical agriculture system. Salt damaged lands found in all climatic

regions and saline soils can be found at different altitudes. Salts are a common and necessary component of soil, and nitrates and potassium are essential plant nutrients. The process of soil salinization is considerably accelerated by crop irrigation. The overall effect of irrigation in the context of salinity is that it imports large amount of salts to the soil. At present about 800 million ha of land is salt affected worldwide (Munns, 2005) and 6 million ha in Pakistan (Chatrath et al., 2007). Pakistan is situated in arid and semi arid region where high evapotranspiration that causes deposition of salts on the soil surface. Salt stress is a major limitation factor to food production as it decrease crop yields and reduce the use of formerly cultivated lands. Pakistan canal irrigated areas especially that in Punjab province are the main contributors to crop production. Salinity problem is becoming more severe in the canal irrigated areas of Pakistan.

Irrigation and poor drainage are main reason of high salt accumulation on land (Zhu, 2007). Irrigation water contains calcium (Ca^{2+}), magnesium (Mg^{2+}), and sodium (Na^+). When the water evaporates, Ca^{2+} and Mg^{2+} frequently precipitate into carbonates, leaving Na^+ dominant in the soil. When Na^+ concentration high in soil solution may depress nutrient-ion activities and produce extreme ratios of $\text{Na}^+/\text{Ca}^{2+}$ or Na^+/K^+ (Grattana and Grieveb, 1999). Increases in cations concentration in soil reduce the influx of water into the root. The resulting water deficit is similar to drought conditions and additionally compounded by the presence of Na^+ ions (Bohnert, 2007). Improper management of salt may cause soil sodicity. Sodium ions when occupy the cation exchange complex of clay particles and it causes soil aggregates to break down. It may increase bulk density, make the soil more compact and decrease total porosity. Plants in saline soils not only suffer from high sodium levels, but are also affected by some degree of hypoxia (Singh and Chatrath, 2001). Saline soil defined by USDA saline soil laboratory as soil having an electrical conductivity of solution extracted from the water-saturated soil paste E_{ce} (Electrical Conductivity of the extract) of 4 dS m^{-1} (decisiemens per meter), where 4 dS m^{-1} or 40 mM NaCl or more. Soil type and environmental factors are major such as vapour, pressure deficit, radiation and temperature may further alter salt tolerance (Zhu, 2007). In fields, the salt levels vary seasonally and spatially, and deviation will occur due to the circumstances influencing each particular plant. In first part of review we focused on impacts of high salt concentration on plant growth. In second part discussion is progress towards the plant tolerance mechanism and how we enhance plants salt tolerance.

Impacts of High Salt on Plants Growth

High salt concentration in soil is a main factor that limits the yield of agricultural crops (Munns and Tester, 2008). When salt concentrations increases causes decrease in yield of glycophytes plants. Halophytes able can survive salinity in excess of 300-400 mM. Halophytes have the capability of growth on salinized soils of coastal. Salt tolerance capacity of these plants can be both obligate and characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% sea water and found in less saline habitats (Parida and Das, 2005). Studies on salt tolerance mechanism raveled that halophytes accumulate salts whereas glycophytes tend to exclude the salts (Zhu, 2007). High salt concentration in soil affects plants in two ways such as high concentrations of salts in the soil upset the ability of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation (Munns and Tester, 2008). A two-phase model describing the osmotic and ionic effects of salt stress was proposed by Munns (1995). Plants response to high salt differs in the rate at which salt reaches toxic levels in leaves. Plant species and the salinity level define plant responses to salt in days and months. In Phase 1 growth of both of plants is less because of the osmotic effect of the saline solution outside the roots. In Phase 2 plants old leaves in the sensitive plant die and reduce the photosynthetic capacity of the plant.

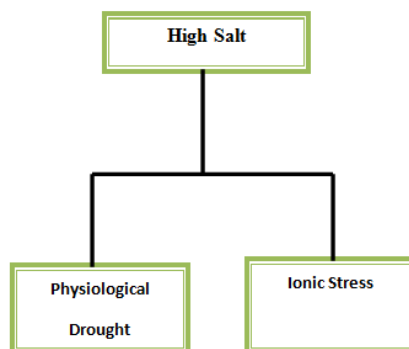


Figure 1. The effect of high salts in soil on Plants

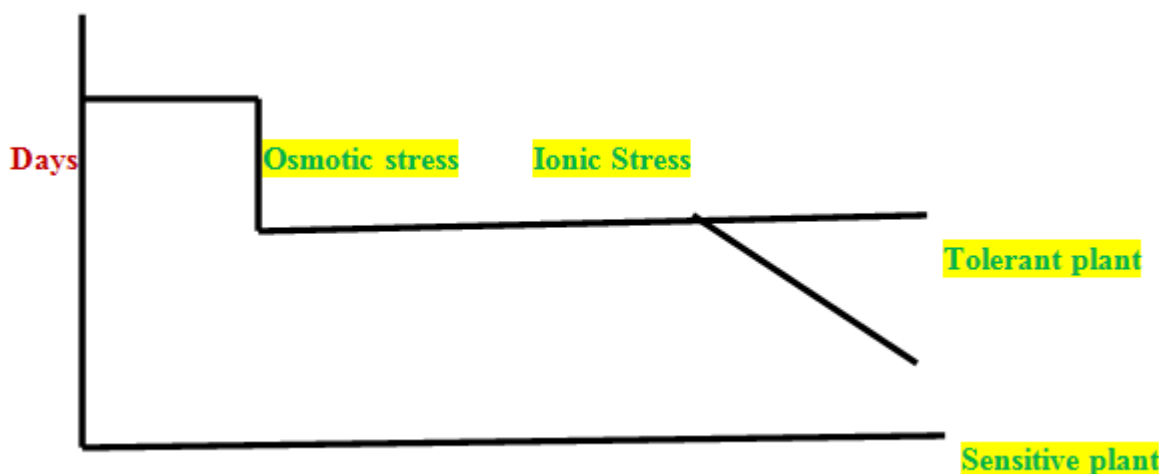


Figure 2. Two phase Model

This exerts an additional effect on growth. In phase 1, high salt concentration around the roots increases to a threshold level making it harder for the roots to extract water, the rate of shoot growth falls considerably. An immediate response to this effect, which also mitigates ion flux to the shoot and promotes stomatal closure. Though, the water potential difference between the atmosphere and leaf cells and the need for carbon fixation, this is an untenable long-term strategy of tolerance (Hasegawa et al., 2000). Shoot growth is more sensitive than root growth to high salt concentration induced osmotic stress possibly because a reduction in the leaf area development relative to root growth would decrease the water use by the plant, thus allowing it to conserve soil moisture and prevent salt concentration in the soil (Munns and Tester, 2008). Reduction in shoot growth due to high salt is frequently expressed by a reduced leaf area and stunted shoots.

The growth inhibition of leaves susceptible to salt stress appears to be also a result of inhibition by salt of symplastic xylem loading of calcium in the root (Läuchli and Grattan, 2007). Leaf size depends on both cell division and cell elongation. Leaf initiation, which is governed by cell division, was shown to be unaffected by salt stress in sugar beet, but leaf extension was found to be a salt-sensitive process. In addition the salt induced inhibition of the uptake of important mineral nutrients, such as potassium and calcium, further reduces root cell growth (Larcher, 1980) and, in particular, compromises root tips expansion. Roots apical region grown under salinity show more vacuolization and lack of typical organization of apical tissue. A slight plasmolysis due to a lack of continuity and adherence between cells is present with a tendency to the arrest of growth and differentiation.

The second phase the accumulation of ions, especially Na^+ in the leaf blade, where Na^+ accumulates after being deposited in the transpiration stream, rather than in the roots (Munns, 2002). Na^+ accumulation turns out to be toxic especially in old leaves. When older leaf no longer expanding as result diluting the salt arriving in them as young growing leaves do. In case the rate at which older leaf die is more than the rate at which new leaves are produced as result plant will no longer be able to supply the carbohydrate requirement of the young leaves which further reduces their growth rate (Munns and Tester, 2008). Sodium accumulation in photosynthetic tissue affects photosynthetic components (Munns, 2005). High sodium accumulation in plants can increase production of reactive oxygen species. Reactive oxygen species are rapidly removed by antioxidative mechanisms (Foyer and Noctor, 2003). Reactive oxygen species playing double role in plants under abiotic stresses functioning as toxic byproducts of stress metabolism and important signal transduction molecules integrated in the networks of stress response pathway mediated by calcium (Miller, 2010). Plant hormones are signal molecules produced in the plant and found in very low concentrations. Abscisic acid plays an important role in the response of plants to salt (Xu, et al., 2001). Salt stress signalling through calcium and Abscisic acid mediate the expression of the late embryogenesis abundant (LEA) genes. The activation of LEA-type genes may actually represent damage repair pathways. Salt and osmotic stress regulation of LEA gene expression is mediated by both ABA dependent and independent signalling pathways. It has been shown that ABA-dependent and -independent transcription factors may also cross talk to each other in a synergistic way to intensify the response and improve stress tolerance.

Tolerance Mechanism Adapted by Plant

Salinity causes considerable reduction in plants growth and production (Rengasamy, 2006; Katerji *et al.*, 2009). Salt tolerance is a complex, quantitative, genetic character controlled by many genes. Genetic control of salt tolerance in plants has not fully understood because of its complexity. There are numerous genes controlling salinity tolerance in the different plant species. Probably the most suitable way to measure plant growth and yield. Salt tolerance can be frequently assessed as the percent biomass production in saline versus control conditions over a prolonged period of time (Munns, 2002). Salt tolerance may vary significantly with genetic traits.

Table 1. Glycophytes and Halophytes tolerance mechanism (reproduce from Parida and Das, 2005)

Halophytes	Glycophytes
1 High water use efficiency	Comparatively less
2 Low level of sodium and chloride ions in cytoplasm	High accumulation
3 Efficiently accumulation of compatible solutes	Low efficiently accumulation
4 Low internal carbon dioxide	Comparatively low

Different mechanisms plants may adapt to acclimatize high salt. Salinity tolerances might increase or decrease depending on the environmental factors and plant species. In some plants salt stress greatest affect at germination stage but some plant species sensitivity may increase during reproduction (Marschner, 1986). Plants have used numerous mechanisms to adapt to salinity. Plant adapted different mechanism of tolerance such as, the tolerance to osmotic stress, the Na⁺ exclusion from leaf blades and accumulation of compatible solutes (Munns and Tester, 2008; James *et al.* 2008). In osmotic tolerance involves plants capacity to tolerate the drought aspect of salinity stress and to maintain leaf expansion and stomatal conductance. When accumulation of salts in older leaf reach to toxic level causes older expanded leaves death, experience a reduction in growth and new leaves production. So we can say that increased osmotic tolerance involves an increased capacity of plant to produce new leaves and higher stomatal conductance. This resulting increased leaf area would advantage only when plants have sufficient soil water but could be undesirable in water limited systems (Munns and Tester, 2008). Whereas osmotic tolerance mechanisms involved to stomatal conductance, water availability and photosynthetic capacity. Sodium ions appears to reach a toxic concentration and so most studies have concentrated on Na⁺ exclusion and the control of Na⁺ transport within the plant (Tester and Davenport, 2003). Consequently mechanism of tolerance involves the capacity to reduce the ionic stress on the plant by minimizing the amount of sodium that accumulates in the cytosol of cells. Sodium exclusion from leaves is associated with salt tolerance in cereal crops. Elimination of sodium from the leaves is due to low net sodium uptake by cells in the root cortex and the tight control of net loading of the xylem by parenchyma cells in the stele. A failure in sodium exclusion manifests its toxic effect after days or weeks, depending on the species, and causes premature death of older leaves (Munns and Tester, 2008).

Cytosolic sodium elimination is also got through operation of vacuolar Na⁺/H⁺ antiports that have the ability to move harmful ions from cytosol into vacuoles. These ions act as an osmoticum within the vacuole and which control water flow into the cell therefore allowing plants to grow in soils containing high salinity. Antiports use the proton motive force generated by vacuolar H⁺-translocating enzymes, H⁺-adenosine triphosphatas and H⁺-inorganic pyrophosphatase (PPiase). Antiports couple downhill movement of hydrogen with uphill movement of sodium (Blumwald, 1999). Wheat is a salt sensitive species especially at germination and seedling stages are the most critical phases. (Davenport and Munns, 2006). The mechanism of sodium exclusion allows the plant to avoid the problem related to ion toxicity if sodium exclusion is not compensated for by the uptake of K⁺ and it determines a greater demand for organic solutes for osmotic adjustment (Munns and Tester, 2008). The knowledge on how Na⁺ is sensed is still very limited in most cellular systems.

Sodium can be sensed before or after entering the cell. Extracellular sodium may be sensed by a membrane receptor, whereas intracellular sodium may be sensed either by membrane proteins or by any of the many sodium sensitive enzymes in the cytoplasm. Plasma membrane Na⁺/H⁺ antiporter salt overly sensitive1 (SOS1) is a possible candidate (Silva and Gerós, 2009). In Arabidopsis, ion homeostasis is mediated chiefly by the SOS signal pathway (Yang *et al.* 2009). SOS proteins are sensor for calcium signal that turn on the machinery for sodium export (Zhu, 2007). SOS1 encoding a plasma membrane Na⁺/H⁺ antiporter plays a significant role in Na⁺ extrusion and in controlling long-distance Na⁺ transport from the root to shoot (Pardo, *et al.*, 2007). Co-expression of SOS1, SOS2, and SOS3 increases the salt tolerance of transformed yeast cells much more than expression of one or two SOS proteins this suggeststhat the full activity of SOS1 depends on the SOS2/SOS3 complex. In recent years SOS4 and SOS5 have also been characterized. The Na⁺ uptake across the plasma membrane has been attributed to low Na⁺ permeability properties of systems that transport essential K⁺ (Blumwald *et al.* , 2000). The vacuolar sodium sequestration is medi-ated by a Na⁺/H⁺ antiport at the tonoplast (Apse *et al.*, 1999).

The third mechanism requires compartmentalization of sodium and chloride at the cellular and intracellular level to avoid toxic concentrations within the cytoplasm particularly in mesophyll cells in the leaf (Munns and Tester, 2008) and accumulation of compatible solutes within the cytoplasm. Compatible solutes play a role in plant osmotolerance. Compatible solutes protect enzymes from denaturation, help in stabilising membrane and macromolecules playing role in mediating osmotic adjustment (Ashraf and Foolad, 2007). The function of the compatible solutes is not limited to osmotic balance. Compatible solutes are hydrophilic nature and may be able to replace water at the surface of proteins. Therefore, they are acting as low molecular weight chaperones. These solutes also function to protect cellular structures through scavenging ROS (Hasegawa et al., 2000). In compatible solutes mostly nitrogen containing compounds such as amino acids, amines and betaines, but also organic acids, sugars and polyols (Mansour, 2000). Glycine betaine is an amphoteric compound that is electrically neutral over a wide range of physiological pH values and is extremely soluble in water despite a non-polar hydrocarbon moiety that consists of three methyl groups. Among the best known compatible solutes proline and glycine betaine (GB) have been reported to increase a great extent under salt and drought stresses (Munns, 2002; Sakamoto and Murata, 2002) and comprise the major metabolites occur in durum wheat under salt stress (Sairam and Tyagi, 2004). The molecular features of GB allow it to not only act as an osmoregulator but also to interact with both hydrophilic and hydrophobic domains of macromolecules, such as protein complexes (Chen et al., 2010; Sakamoto and Murata 2002). It has also been suggested that GB plays a role as a scavenger of ROS generated during these various stresses (Ashraf and Foolad 2007). Proline is amino acid with an excellent conformational rigidity this essential for primary metabolism. This normally accumulates in large quantities in response to drought or salinity stress (Ashraf and Foolad, 2007, Szabados and Savoure, 2010). In many halophytes proline and glycine betaine concentrations in leaves contribute to the osmotic pressure in the cell as a whole. In glycophytes, their concentrations are much lower but if partitioned exclusively to the cytoplasm, they could generate a significant osmotic pressure and then balance the vacuolar osmotic potential (Carillo et al. 2008). Its accumulation normally occurs in the cytosol where it contributes substantially to the cytoplasmic osmotic adjustment. Proline accumulation is due primarily to de novo synthesis associated with decreased oxidation and utilization but increased transport processes are also likely involved. Proline accumulation occurs rapidly after the onset of stress and this supports the hypothesis that this accumulation is initially a reaction to salt stress and not a plant response associated with tolerance. In addition to its role as an osmolyte for osmotic adjustment, proline contributes to stabilizing sub-cellular structures, scavenging free radicals and buffering cellular redox potential under stress conditions. It may also function as a protein compatible hydrotrope (Hare and Cress, 1997). Rapid breakdown of proline upon relief of stress may give sufficient reducing agents that support mitochondrial oxidative phosphorylation and generation of ATP for recovery from stress and repairing of stress-induced damages. In addition, proline is known to induce expression of salt stress responsive genes (Ashraf and Foolad, 2007). Though proline is most widely distributed osmolyte accumulated in plants (Szabados and Savoure 2010), the occurrence of GB seems to be restricted to several halophytes and a few crop plants. Metabolic engineering of GB biosynthesis by the insertion of foreign genes from plants helps to improved their tolerance to abiotic stress (Ashraf and Akram, 2009). Addition of cyclic polyols such as 1D-3-O-methyl-chiro-inositol or 1D-4-O-methyl-myo-inositol has regularly been reported in response to drought and salinity. Numerous physiological studies suggested that under stress conditions nonstructural carbohydrates accumulate though to varying degree in different plant species. A strong correlation among sugar accumulation and osmotic stress tolerance has been broadly reported including transgenic experiments.

Enhancement Strategies

Several scientists are trying to improve salt tolerance of plants by traditional plant breeding as well as by biotechnological approaches. Traditional breeding programs to improve abiotic stress tolerance have had some success but are progressing relatively slow being limited by the polygenic inheritance. Tolerance to salinity in plants is a coordinated action of multiple stress responsive genes. They also cross talk with other components of stress signal transduction pathways. Quantitative trait loci mapping studies that represent the extremes of a trait are used for mapping. Breeding efficiency and future development of new superior cultivars will depend on the use of efficient marker-assisted selection strategies. Molecular marker technology has developed rapidly over the last decade with the development of high throughput genotyping methods that have made it possible to analyze the QTL responsible for tolerance. When we were identify these regions helping for the selection efficiency in breeding programs and mapping the major genes controlling salt tolerance in order to operate genetic manipulations using the real candidate genes rather than non-specific abiotic responsive genes. QTLs mapping for salt tolerance related traits in rice because of its requirement for irrigation for maximum yield, its sensitivity to salinity and its relatively small genome. Better results have been obtained at the seedling stage, while the expression but difficult

to detect relationship of QTLs in different developmental stages (Tumimbang-Raiz, et al., 2011). QTLs related to antioxidant content and the response of tomato antioxidants to salt stress has also been identified. Transgenic plants over expressing the genes participating in the synthesis and accumulation of osmoprotectants that function for osmotic adjustment such as proline, glycinebetaine, mannitol, fructan and pinitol show increased salt tolerance. Other genes that might encode enzymes that are involved in oxidative defense in which include glutathione S-transferase, peroxidase, superoxide dismutase, ascorbate peroxidases, and glutathione reductases can also be modified to improve plant salt tolerance.

Regulatory genes DREB/CBF, MAPK and CDPK overexpression in signalling pathway also increase plant salt tolerance. Vacuolar Na⁺/H⁺ antiporter has shown to improve salinity tolerance in several plants (Silva and Geros, 2009). Transgenic tomato plants overexpressing AtNHX1 were able to grow even produce flower and fruit in the presence of 200 mM NaCl (Foolad, 2004). In *Petunia hybrida* overexpression of AtNHX1 enhanced salt and water stress tolerance. This help to accumulate more sodium, potassium and proline in their leaf tissue than that of the wild *Petunia* plants (Xia et al., 2009). In cereal crops introgressing Nax genes from *Triticum monococcum* into hexaploid bread wheat (*Triticum aestivum*) helps plant to reduce Na⁺ concentration in leaf blade about 60% and the proportion of sodium stored in leaf sheaths was increased. The results indicate that Nax genes have the potential to improve the salt tolerance of bread wheat. In tomato and rice overexpression of Arginine Vasopressin 1 (AVP1) gene of Arabidopsis helps to encode a vacuolar pyrophosphatase acting as a proton pump on the vacuolar membrane and increased sequestering of ions into the vacuole. This may help to increased salt tolerance when compared to wild type plants (Hou, et al., 2011). In addition to this Late Embryogenesis Abundant (LEA) genes are encoding Late Embryogenesis Abundant (LEA) proteins. This protein help plant to accumulate solutes during seed development and wheat dehydrin DHN-5 (Brini et al., 2007) can enhance plant salt tolerance but still their function is unclear. Salt stress requires changes in water flow to allow cells and tissue to adapt to the stress situation. Aquaporin proteins make possible osmosis by forming water specific pores as an alternative to water diffusion throughout the lipid bilayer. In plants, aquaporins localized in the tonoplast are called tonoplast intrinsic proteins TIP, while those in the plasma membrane are PIP. Polyamines role has been proposed in stress responses. Salt tolerant Pokkali rice plants accumulate higher levels of polyamines compared to the salt sensitive rice plants in response to salinity stress (Chattopadhyay et al., 2002).

Table 2. Salt tolerance in transgenic plants expressing genes involved in ion transport (reproduce from Yamaguchi and Blumwald, 2005)

Gene	Gene product	Plant source	Role	Transgenic plant	Parameter
AtNHX1	Vacuolar Na/H antiporter	Arabidopsis	Sodium sequestration	Arabidopsis	Biomass
AtNHX1	Vacuolar Na/H antiporter	Arabidopsis	Sodium sequestration	Tomato	Biomass, fruit yield
AtNHX1	Vacuolar Na/H antiporter	Arabidopsis	Sodium sequestration	Canola	Biomass, oil production
AtNHX1	Vacuolar Na/H antiporter	Arabidopsis	Sodium sequestration	Maize	Biomass
AtNHX1	Vacuolar Na/H antiporter	Arabidopsis	Sodium sequestration	Wheat	Biomass, grain yield
GhNHX1	Vacuolar Na/H antiporter	Gossypium hirsutum	Sodium sequestration	Tobacco	Biomass
AgNHX1	Vacuolar Na/H antiporter	Atriplex gmelini	Sodium sequestration	Rice	Biomass
OsNHX1	Vacuolar Na/H antiporter	Oryza sativa	Sodium sequestration	Rice	Growth, ion content
BnNHX1	Vacuolar Na/H antiporter	Brassica napus	Sodium sequestration	Tobacco	Growth, seed yield
HbNHX1	Vacuolar Na/H antiporter	Hordeum	Sodium sequestration	Tobacco	Biomass
AtSOS1	Plasma membrane Na/H antiporter	Arabidopsis	Sodium extrusion	Arabidopsis	Biomass
SOD2	Plasma membrane Na/H antiporter	Schizosaccharomyces	Sodium extrusion	Arabidopsis	Biomass, photosynthesis
nhaA	Plasma membrane Na/H antiporter	E. coli	Sodium extrusion	Rice	Biomass, ion content
AVP1	Vacuolar H pyrophosphates	Arabidopsis	Vacuolar acidification	Arabidopsis	Biomass

CONCLUSIONS

Salinity is an important problem affecting agriculture worldwide and is predicted to become a larger problem in the coming decades. 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. Some plant species are clearly more flexible than others in their requirements for survival in salty environments. An understanding of how single cell responses to salt are coordinated with organismal and whole-plant responses to maintain an optimal balance between salt uptake and compartmentation is fundamental to our knowledge of how plants successfully adapt to salt stress. Use of both genetic manipulation and traditional breeding approaches will be required to unravel the mechanisms involved in salinity tolerance and to develop salt-tolerant cultivars better able to cope with the increasing soil salinity constraints. Though, a combination of such master genes that act in different pathways ROS scavenging and osmotic adaptation may prove even more beneficial for improving stress tolerance.

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