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Review Article

Effect of salinity stress on plants and its tolerance strategies: a review

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Abstract

The environmental stress is a major area of scientific concern because it constraints plant as well as crop productivity. This situation has been further worsened by anthropogenic activities. Therefore, there is a much scientific saddle on researchers to enhance crop productivity under environmental stress in order to cope with the increasing food demands. The abiotic stresses such as salinity, drought, cold, and heat negatively influence the survival, biomass production and yield of staple food crops. According to an estimate of FAO, over 6 % of the world's land is affected by salinity. Thus, salinity stress appears to be a major constraint to plant and crop productivity. Here, we review our understanding of salinity impact on various aspects of plant metabolism and its tolerance strategies in plants.

Keywords Genomics – Metabolomics – Plant productivity – Proteomics – Salinity stress – Salinity tolerance – Transcriptomics

Introduction

Stress is defined as any external abiotic (salinity, heat, water, etc.) or biotic (herbivore) constraint that limits the rate of photosynthesis and reduces a plant's ability to convert energy to biomass (Grime 1977). World agriculture is facing a lot of challenges like producing 70 % more food for the growing population and the productivity of crops is not increasing in parallel with the food demand. The lower productivity in most of the cases is attributed to various abiotic stresses. Curtailing crop losses due to various environmental stressors is a major area of concern to cope with the increasing food requirements (Shanker and Venkateswarlu 2011). The major abiotic stresses like high salinity, drought, cold, and heat negatively influence the survival, biomass production, and yield of staple food crops up to 70 % (Vorasoot et al. 2003; Kaur et al. 2008; Ahmad et al. 2010a; Thakur et al. 2010; Mantri et al. 2012; Ahmad et al. 2012). The adverse effect of excess minerals such as Na⁺ and/or Cl⁻ on plant is called salt stress (Munns 2005). It has been shown that soil salinity subsisted long before humans and agriculture; however, the problem has been arisen by agricultural practices such as irrigation (Zhu 2001). Salt stress is one of the most serious limiting factors for crop growth and production. Based on the nature, characteristics, and plant growth relationships in

salt affected soils, two main types of soils have been coined by Szabolcs (1974). These are (1) saline soils—the soluble salts are chiefly NaCl and Na₂SO₄ and sometimes also contain appreciable quantities of Cl⁻ and SO₄⁻ of Ca²⁺ and Mg²⁺; these soils contain sufficient neutral soluble salts to pose negative effect on growth of most crop plants, and (2) sodic soils—these soils contain Na⁺ salts capable of alkaline hydrolysis, mainly Na₂CO₃. In this review article, type and causes of salinity, impact of salinity on plants, and salt tolerance strategies of plants are discussed.

Types and causes of salinity

Natural or primary salinity

Primary salinity results from the accumulation of salts over long periods of time through natural processes in the soil or groundwater. It is caused by two natural processes. The first is the weathering of parent materials containing soluble salts. Weathering processes break down rocks and release soluble salts of various types mainly chlorides of sodium, calcium, and magnesium, and to a lesser extent, sulfates and carbonates. Sodium chloride is the most soluble salt. The second is the deposition of oceanic salt carried in wind and rain. “Cyclic salts” are ocean salts carried inland by wind and deposited by rainfall and are mainly sodium chloride.

Secondary or human-induced salinity

Secondary salinization results from human activities that change the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration; Garg and Manchanda 2008). The most common causes are (a) land clearing and the replacement of perennial vegetation with annual crops and (b) irrigation schemes using salt-rich irrigation water or having insufficient drainage.

According to the FAO Land and Plant Nutrition Management Service, over 6 % of the world’s land is affected by salinity. Of the current 230 million hectares of irrigated land, 45 million hectares is salt-affected (19.5 %), and of the 1,500 million hectares under dry land agriculture, 32 million are salt-affected to varying degrees (2.1 %). Table 1 shows that the proportion of salt-

affected irrigated land in various countries ranges from a minimum of 9 % to a maximum of 34 %, with a world average of 20 %. Irrigated land is only 15 % of total cultivated land, but as irrigated land has at least twice the productivity of rain-fed land, it may produce one third of the world's food.

Table 1

Global estimate of secondary salinization in the world's irrigated soils (source Ghassemi et al. 1995)

Country	Total land area cropped	Area irrigated		Area of irrigated land that is salt affected	
	Mha	Mha	%	Mha	%
China	97	45	46	6.7	15
India	169	42	25	7.0	17
Soviet Union	233	21	9	3.7	18
United States	190	18	10	4.2	23
Pakistan	21	16	78	4.2	26
Iran	15	6	39	1.7	30
Thailand	20	4	20	0.4	10
Egypt	3	3	100	0.9	33
Australia	47	2	4	0.2	9
Argentina	36	2	5	0.6	34
South Africa	13	1	9	0.1	9
Subtotal	843	159	19	29.6	20
World	1,474	227	15	45.4	20

Irrigation water adds appreciable amounts of salt even with good quality irrigation water containing only 200–500 mg/kg of soluble salt. Irrigation water with a salt content of 500 mg/kg (i.e., 500 mg/l) contains 0.5 tons of salt per 1,000 m³. Since crops

require 6,000–10,000 m³ of water per hectare each year, 1 ha of land will receive 3–5 tons of salt. Because the amount of salt removed by crops is negligible, salt will accumulate in the root zone and must be leached by supplying more water than is required by the crops. If drainage is not adequate, the excess water causes the water table to rise, mobilizing salts which accumulate in the root zone. When the crop is unable to use all the applied water, water logging occurs.

The effects of salinity on plants

Salts in the soil water may inhibit plant growth for two reasons. Firstly, the presence of salt in the soil solution reduces the ability of the plant to take up water and this leads to reductions in the growth rate. This is referred to as the osmotic or water-deficit effect of salinity. Secondly, if excessive amounts of salt enter the plant in the transpiration stream, there will be injury to cells in the transpiring leaves and this may cause further reductions in growth. This is called the salt-specific or ion-excess effect of salinity (Greenway and Munns 1980). These salinity effects has threefold effects *viz.* it reduces water potential and causes ion imbalance or disturbances in ion homeostasis and toxicity; this altered water status leads to initial growth reduction and limitation of plant productivity. The detrimental effect is observed at the whole-plant level as death of plants or decrease in productivity. Salt stress affects all the major processes such as germination, growth, photosynthetic pigments and photosynthesis, water relation, nutrient imbalance, oxidative stress, and yield. These are discussed under separate headings.

Germination

Seed germination is one of the most fundamental and vital phases in the growth cycle of a plant that determines the yield. However, it has been established that salinity adversely affects the process of germination in various plants like *Posidonia* (Fernández-Torquemada and Sánchez-Lizaso 2013), *Oryza sativa* (Xu et al. 2011), *Triticum aestivum* (Akbarimoghaddam et al. 2011), *Zea mays* (Carpıcı et al. 2009; Khodarahmpour et al. 2012), and *Brassica* spp. (Ibrar et al. 2003; Ulfat et al. 2007). Salinity affects the germination process many-folds. It alters the imbibitions of water by seeds due to lower osmotic potential of germination media (Khan and Weber 2008), causes toxicity which changes the activities of enzymes of nucleic acid metabolism (Gomes-Filho et al. 2008), alters protein metabolism (Dantas et al. 2007), disturbs hormonal balance (Khan and Rizvi 1994),

and reduces the utilization of seed reserves (Othman et al. 2006). The germination rates and percentage of germinated seeds at a particular time vary considerably among species and cultivars. Lauchli and Grattan (2007) proposed a generalized relationship between percent germination and time after adding water at different salt levels (Fig. 1). Kaveh et al. (2011) found a significant negative correlation between salinity and the rate and percentage of germination which resulted in delayed germination and reduced germination percentage in *Solanum lycopersicum*. Bordi (2010) reported that the germination percentage in *Brassica napus* significantly reduced at 150 and 200 mM NaCl. Germination rate also decreased on increasing concentration of salinity levels. Compared with control, germination percentage, and germination speed were decreased by 38 and 33, respectively, at 200 mM NaCl. In a recent study, Khodarahmpour et al. (2012) observed drastic reduction in germination rate (32 %), length of radicle (80 %) and plumule (78 %), seedling length (78), and seed vigor (95 %) in *Z. mays* seeds exposed to 240 mM NaCl.

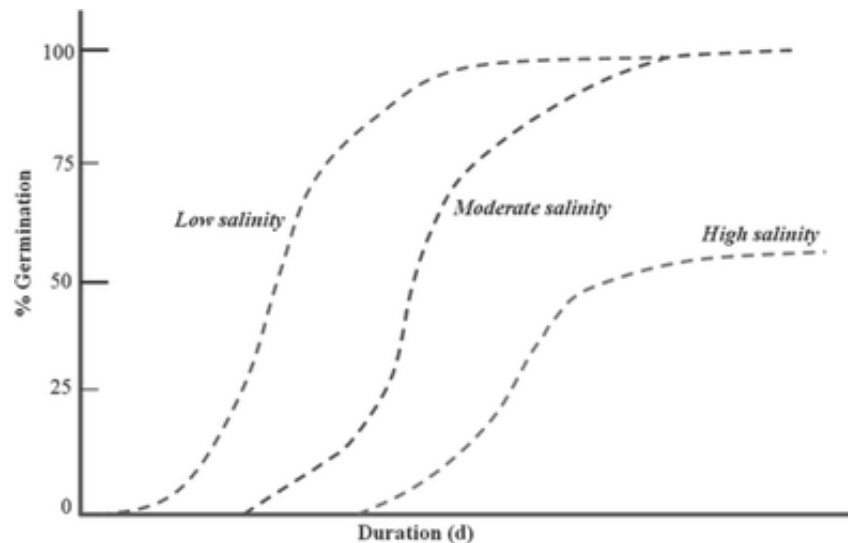


Fig. 1

Relationship between rate of germination and time after sowing at different salinity levels (adopted from Lauchli and Grattan 2007)

Growth

One of the initial effects of salt stress is the reduction of growth rate. Salt in soil water inhibits plant growth for two reasons.

First, it reduces the plant's ability to take up water and this leads to slower growth. This is the osmotic or water-deficit effect of

salinity. Second, it may enter the transpiration stream and eventually injure cells in the transpiring leaves, further reducing growth. This is the salt-specific or ion-excess effect of salinity. The two effects give rise to a two-phase growth response to salinity given by Munns (1993, 2005; Fig. 2).

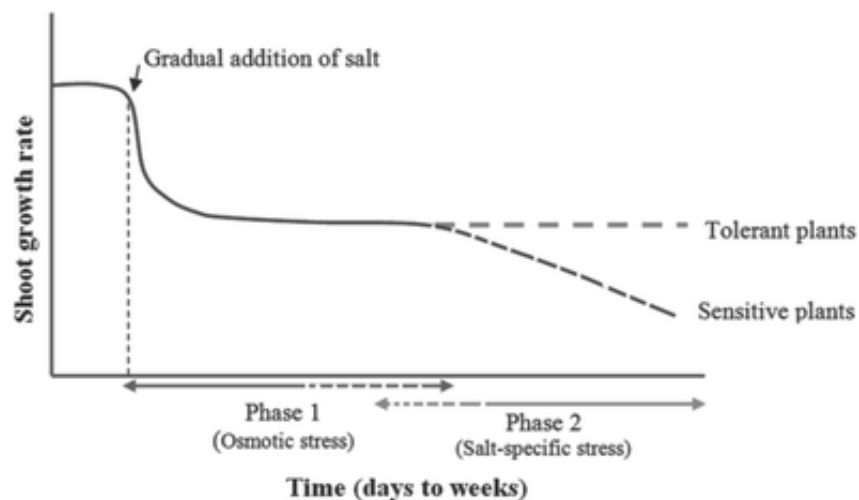


Fig. 2

Overview of the two-phase growth response to salinity for plant differing in salt sensitivity (adopted from Munns 2005)

Phase 1: The first phase of the growth response results from the effect of salt outside the plant. The salt in the soil solution reduces leaf growth and to a lesser extent root growth (Munns 1993). The cellular and metabolic processes involved are in common to drought-affected plants. Neither Na^+ nor Cl^- builds up in growing tissues at concentrations that inhibit growth: meristematic tissues are fed largely in the phloem from which salt is effectively excluded, and rapidly elongating cells can accommodate the salt that arrives in the xylem within their expanding vacuoles.

Phase 2: The second phase of the growth response results from the toxic effect of salt inside the plant. The salt taken up by the plant concentrates in old leaves: continued transport into transpiring leaves over a long period eventually results in very high Na^+ and Cl^- concentrations, and the leaves die. The cause of injury is probably the salt load exceeding the ability of cells to compartmentalize salts in the vacuole. Salts would then build up rapidly in the cytoplasm and inhibit enzyme activity.

Alternatively, they might build up in the cell walls and dehydrate the cell. The excessive salt concentration correspondingly

increases the osmotic potential of the soil that restricts the water uptake by plants. The Na^+ and Cl^- ions are the major ions that produce many physiological disorders and detrimental effects on plants. However, Na^+ is the primary ion as it interferes with the uptake of potassium (K^+) ion and disturbs stomatal regulation that ultimately causes water loss while the Cl^- ion disturbs the chlorophyll production and causes chlorotic toxicity. But, Cl^- is more dangerous than Na^+ (Tavakkoli et al. 2011). Moreover, the need of Cl^- in plant is essential as well and is required for the regulation of turgor pressure and pH and enzyme activities in the cytoplasm. Dang et al. (2008), on the basis of number of field trials, concluded that Cl^- concentration in the soil was more important to growth and yield reduction than Na^+ and the critical level (defined as the concentration that reduces the growth or yield by 10 %) of subsoil Cl^- concentration was estimated to be $490 \text{ mg Cl}^- \text{ kg}^{-1}$ soil. The Cl^- concentration in the youngest mature leaf of bread wheat, durum wheat, and chickpea showed greater variability with increasing levels of subsoil constraints than Na^+ concentration (Dang et al. 2006). However, it is toxic to plants at high concentrations with critical levels for toxicity reported to be $4\text{--}7 \text{ mg g}^{-1}$ for Cl^- -sensitive species and $15\text{--}50 \text{ mg g}^{-1}$ for Cl^- -tolerant species (Xu et al. 2000; White and Broadley 2001).

Salinity and ionic toxicity

The presence of excessive soluble salts in the soil competes with the uptake and metabolism of mineral nutrient that are essential to plants (Fig. 3). The appropriate ion ratios provide a tool to the physiological response of a plant in relation to its growth and development (Wang et al. 2003). However, increased salt uptake induces specific ion toxicities like that of high Na^+ , Cl^- , or sulfate (SO_4^{2-}) that decrease the uptake of essential nutrients like phosphorus (P), potassium (K^+), nitrogen (N), and calcium (Ca^{++} ; Zhu 2001). Salinity enhances the Na^+ content in *Vicia faba* while the Na^+/K^+ ratio was decreased (Gadallah 1999) thus suggesting a negative relationship between Na^+ and K^+ . In addition, many of the deleterious effects of Na^+ seem to be related to the structural and functional integrity of membranes (Kurth et al. 1986). Salinity stress causes an increase in the levels of Na^+ and Cl^- in *Atriplex griffithii* in root, stem, as well as in leaves, and the highest ion accumulation was found in leaves followed by stem and root suggesting a positive relationship between Na^+ and Cl^- concentration. The Ca^{2+} content was reduced in shoots and leaves of *A. griffithii* plants grown at high salinity; however, being stable in roots and the K^+ content was reduced with increased levels of salinity, particularly in leaves. On the other hand, Mg^{2+} concentration was not much affected in stems and roots but the decrease in leaf was more prominent (Khan et al 2000). Decrease in Ca^{2+} and Mg^{2+} content of leaves upon salinity stress suggests increased membrane stability and decreased chlorophyll content, respectively (Parida et al. 2004). Despite the fact that

most plants accumulate both Na^+ and Cl^- ions in high concentrations in their shoot tissues when grown in saline soils, Cl^- toxicity is also an important cause of growth reduction. Tavakkoli et al. (2011) studied the extent to which specific ion toxicity of Na^+ and Cl^- reduces the growth of four barley genotypes grown in saline soils under varying salinity treatments. High Na^+ , Cl^- , and NaCl separately reduced the growth of barley; however, the reductions in growth and photosynthesis were greatest under NaCl stress and were mainly additives of the effects of Na^+ and Cl^- stress. They also reported that Na^+ and Cl^- exclusion among barley genotypes are independent mechanisms and different genotypes expressed different combinations of the two mechanisms. High concentrations of Na^+ reduced K^+ and Ca^{2+} uptake and reduced photosynthesis mainly by reducing stomatal conductance, while high Cl^- concentration reduced the photosynthetic capacity due to non-stomatal effects and chlorophyll degradation (Tavakkoli et al. 2011).

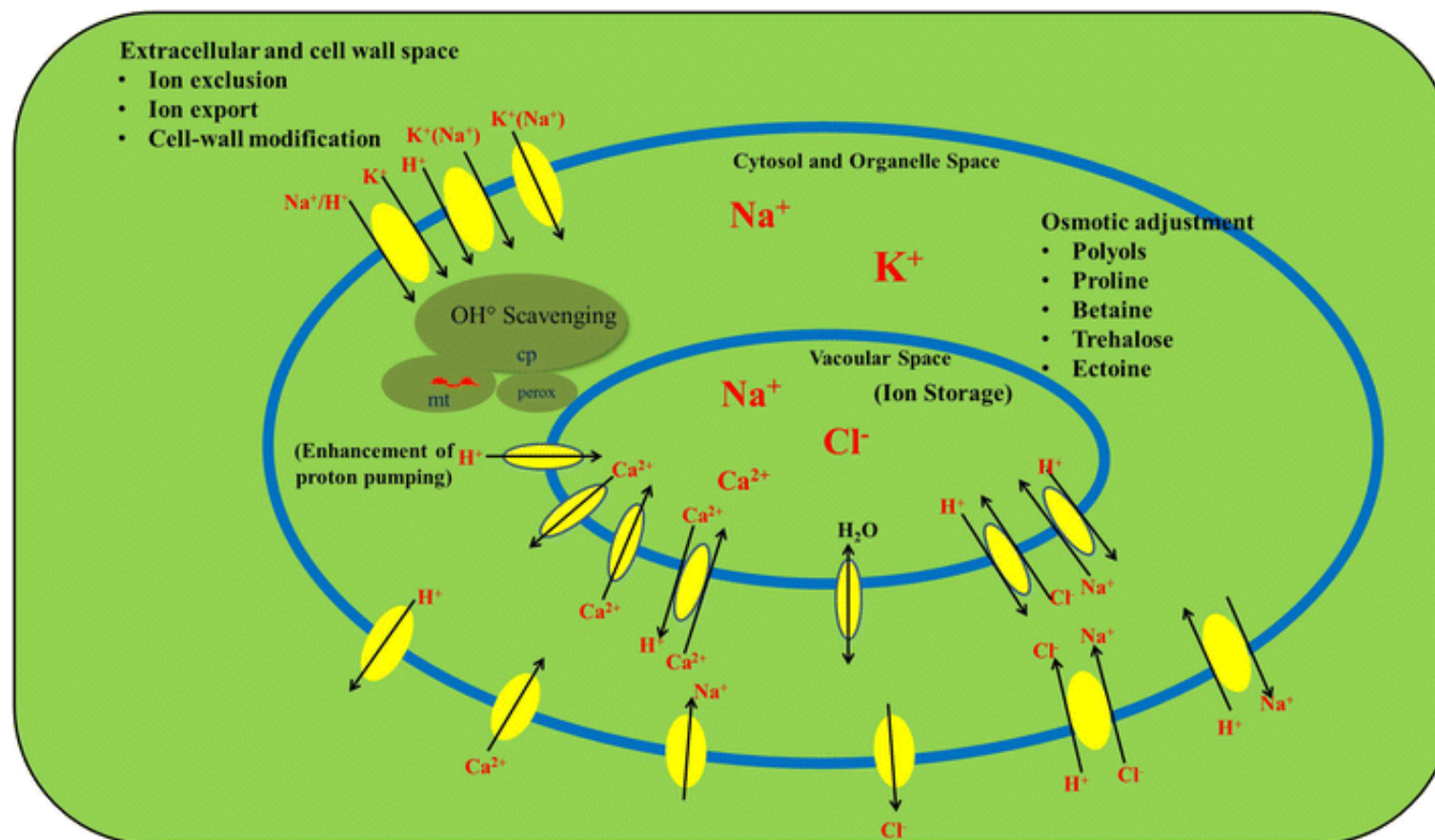


Fig. 3

The schematic presentation of a plant cell includes three compartments that are defined by the extracellular space; cytosolic space and vacuolar space. Indicated are the osmolytes and ions compartmentalized in the cytoplasm and vacuole, and transport proteins responsible for Na^+ and Cl^- homeostasis across the plasma membrane and tonoplast. Included are organelles (chloroplast (chlcp), mitochondrion (mitmt), and peroxisome (perox)) for which the importance of ROS-scavenging is implicated

There is abundant literature indicating that plants are particularly susceptible to salinity during the seedling and early vegetative growth stage. One of the studies in *O. sativa* showed a remarkable reduction in plant height and tiller number and leaf area index in plants grown in saline soil (Hasanuzzaman et al. 2009). In *Suaeda salsa*, plant height, number of branches, length of branches, and diameter of shoot were significantly affected by salt stress which was due to the increased content of Na^+ and Cl^- (Guan et al. 2011). While studying with *Glycine max*, Dolatabadian et al. (2011) observed that salinity stress significantly decreased shoot and root weight, total biomass, plant height, and leaf number. In one of the recent studies on *Foeniculum vulgare*, it has been shown that yields and plant growth parameters including plant height, fresh weight, yield, and biomass were affected significantly by irrigation water salinities at 0.01 probability levels (Semiz et al. 2012). However, there are many mechanisms that plants employ to combat the salt stress, retain homeostasis, and overcome ion toxicity (Zhu 2001; Parida et al. 2005). Some of these mechanisms include restriction of the mechanisms involved in salt uptake, control of long distance transport of salt, compartmentalization of salt, extrusion of salt from the plant, and prioritization of the maintenance of K/Na^+ ratio in the cytosol (Fig. 3).

Photosynthetic pigments and photosynthesis

Photosynthesis is one of the most important biochemical pathways by which plants convert solar energy into chemical energy and grow. The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of Na^+ and/or Cl^- are accumulated in the chloroplasts and chlorophyll being important content of photosynthesis directly correlates to the healthiness of plant (Zhang et al. 2005). The decrease in chlorophyll content under salt stress is a commonly reported phenomenon, and in various studies, chlorophyll concentration has been used as a sensitive indicator of the cellular metabolic state (Chutipaijit et al. 2011). In *O. sativa* leaves, the reduction of chlorophyll *a* and *b* contents of leaves was observed after NaCl treatment (200 mM NaCl, 14 days) where chlorophyll *b* content of leaves (41 %) was affected more than the chlorophyll *a* content (33 %) (Amirjani 2011). In another study, *O. sativa* exposed

to 100 mM NaCl showed 30, 45, and 36 % reduction in chlorophyll *a*, chlorophyll *b*, and carotenoids contents as compared to the control (Chutipaijit et al. 2011). Saha et al. (2010) observed a linear decrease in the levels of total chlorophyll, chlorophyll *a*, chlorophyll *b*, carotenoids, and xanthophylls as well as the intensity of chlorophyll fluorescence in *Vigna radiata* under increasing concentrations of NaCl treatments. Compared to control, the pigment contents decreased on an average by 31 % for total chlorophyll, 22 % for chlorophyll *a*, 45 % for chlorophyll *b*, 14 % for carotene, and 19 % for xanthophylls (Saha et al. 2010). In one of the studies in cucumber, it has been shown that total leaf chlorophyll contents significantly decreased with an increasing NaCl levels. The decrease in total chlorophyll contents was 12, 21, and 30 % at 2 and 3, and 5 dS m⁻¹ of salt stress, respectively, compared to non-treated plants (Khan et al. 2013). Associated with the decline in pigment levels, there was an average 16 % loss of the intensity of chlorophyll fluorescence as well. Usually, there is dominance of chlorophyll “*a*” over chlorophyll “*b*” in plants but their values become closer with increasing salinity (Mane et al. 2010). The decrease in chlorophyll content under stress is a commonly reported phenomenon, and in various studies, this may be due to different reasons, one of them is related to membrane deterioration (Mane et al. 2010).

Photosystem II (PS II) is a relatively sensitive component of the photosynthetic system with respect to salt stress (Allakhverdiev et al. 2000). A considerable decrease in the efficiency of PS II, electron transport chain (ETC), and assimilation rate of CO₂ under the influence of salinity has been noticed (Piotr and Grazyna 2005). Demetriou et al. (2007) noticed alterations in photosynthetic characteristics of *Scenedesmus obliquus* that result into declined biomass accumulation. In citrus, salinity stress decreased growth by reducing of net photosynthetic rate, stomatal conductance, performance of PSII, and photosynthetic efficiency (López-Climent et al. 2008). Kalaji et al. (2011) reported that salinity stress affects growth of barley by altering chlorophyll fluorescence (PS II) and function of oxygen evolving complex. Furthermore, Mittal et al. (2012) observed that salt stress affects growth of *Brassica juncea* by affecting photosynthetic (PS II) and electron transport rates, and D1 protein. There are some other factors that reduce photosynthetic rates under salt stress: dehydration of cell membranes which reduce their permeability to carbon dioxide, salt toxicity, enhanced senescence, changes in enzyme activity induced by alterations in cytoplasmic structure, and negative feedback by reduced sink activity (Iyengar and Reddy 1996).

Water relation

Water potential is an important physiological parameter for determining the water status of the plants (Parida and Das 2005).

According to Romero-Aranda et al. (2001), an increase of salt in the root medium can lead to a decrease in leaf water potential and, hence, may affect many plant processes. At very low soil water potentials, this condition interferes with plant's ability to extract water from the soil and maintain turgor. However, at low or moderate salt concentration (higher soil water potential), plants adjust osmotically (accumulate solutes) and maintain a potential gradient for the influx of water. In one of the experiments in *Cucumis sativa*, it has been shown that the water potential decreases linearly with increasing salinity levels (Khan et al. 2013).

Nutrient imbalance

It is well-established that crop performance may be adversely affected by salinity-induced nutritional disorders. However, the relations between salinity and mineral nutrition of crops are very complex (Grattan and Grieve 1999). The nutritional disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport, or distribution within the plant. Numerous reports indicated that salinity reduces nutrient uptake and accumulation of nutrients into the plants (Rogers et al. 2003; Hu and Schmidhalter 2005). The availability of micronutrients in saline soils is dependent on the solubility of micronutrients, the pH of soil solution, redox potential of the soil solution, and the nature of binding sites on the organic and inorganic particle surfaces. In addition, salinity can differently affect the micronutrient concentrations in plants depending upon crop species and salinity levels (Oertli 1991). Micronutrient deficiencies are very common under salt stress because of high pH (Zhu et al. 2004). Numerous plant studies have demonstrated that salinity could reduce nitrogen accumulation in plants. Decreased N uptake under saline conditions occurs due to interaction between Na^+ and NH_4^+ and/or between Cl^- and NO_3^- that ultimately reduce the growth and yield of the crop (Rozeff 1995). This reduction in NO_3^- uptake is associated with Cl^- antagonism (Bar et al. 1997) or reduced water uptake under saline conditions (Lea-Cox and Syvertsen 1993). The availability of phosphorus is also reduced in saline soil due to (a) ionic strength effects that reduced the activity of PO_4^{3-} , (b) phosphate concentrations in soil solution was tightly controlled by sorption processes, and (c) low solubility of Ca-P minerals. Hence, it is noteworthy that phosphate concentration in agronomic crops decreases as salinity increases (Qadir and Schubert 2002). Sodium concentration in plant tissues increases in the high NaCl treatment and Leaf Ca^{2+} , K^+ , and N decreases (Tuna et al. 2007). Elevated sodium chloride (NaCl) levels in the root medium reduce the nutrient assimilation, especially of K and Ca, resulting in ion imbalances of K, Ca, and Mg (Keutgen and Pawelzik 2009). In a recent study, it has been reported that Ca^{2+} and Mg^{2+} concentrations of all plant organs transiently declined in response to external NaCl salinity (Hussin et al. 2013).

Salinity and oxidative stress

Besides direct impact of salinity on plants, a common consequence of salinity is induction of excessive accumulation of reactive oxygen species (ROS) which can cause peroxidation of lipids, oxidation of protein, inactivation of enzymes, DNA damage, and/or interact with other vital constituents of plant cells. Salt stress can lead to stomatal closure, which reduces carbon dioxide availability in the leaves and inhibits carbon fixation, exposing chloroplasts to excessive excitation energy which in turn increase the generation of ROS such as superoxide ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^{\bullet}), and singlet oxygen (1O_2 ; Parida and Das 2005; Ahmad and Sharma 2008; Ahmad et al. 2010a, 2011). On the other hand, as salt stress is complex and imposes a water deficit because of osmotic effects on a wide variety of metabolic activities (Greenway and Munns 1980; Cheeseman 1988). This water deficit leads to the formation of ROS (Halliwell and Gutteridge 1985; Elstner 1987). ROS are highly reactive and may cause cellular damage through oxidation of lipids, proteins, and nucleic acids (Apel and Hirt 2004; Ahmad et al. 2010a,b). In many plant studies, it was observed that production of ROS is increased under saline conditions and ROS-mediated membrane damage has been demonstrated to be a major cause of the cellular toxicity by salinity in different crop plants such as rice, tomato, citrus, pea, and mustard (Gueta-Dahan et al. 1997; Dionisio-Sese and Tobita 1998; Mittova et al. 2004; Ahmad et al. 2009, 2010b). In one of the studies, it has been shown that long-term salinity treatments (EC 5.4 and 10.6 dS m⁻¹, 60 days) causes significant increase in H_2O_2 and lipid peroxidation in wheat seedlings, which was higher in salt-sensitive cultivar than salt tolerant cultivar (Sairam et al. 2002). In a recent study, increased lipid peroxidation and levels of H_2O_2 were observed with increased salinity in *Brassica napus* (Hasanuzzaman and Fujita 2011a) and *Triticum aestivum* (Hasanuzzaman and Fujita (2011b)). It has been shown that the production of ROS during environmental stresses such as salinity is one of the main causes for decreases in crop productivity (Halliwell and Gutteridge 1989; Asada 1994). Therefore, regulation of ROS is a crucial process to avoid unwanted cellular cytotoxicity and oxidative damage (Halliwell and Gutteridge 1989).

Yield

The above mentioned effects of salt stress on plants ultimately lead to reduction of yield of crop which is the most countable effect of salt stress in agriculture. Different yield components of *Vigna radiate* were significantly affected by salinity stress as reported by Nahar and Hasanuzzaman (2009). Numbers of pods per plant, seeds per pod, and seed weight were negatively

correlated with salinity levels. The reproductive growth of *V. radiata* was also affected by salinity as the number of pods per plant substantially decreased with increasing salinity levels. An application of 250 mM NaCl reduced 77, 73, and 66 % yield in *V. radiata* cv. BARI mung-2, BARI mung-5, and BARI mung-6, respectively over control (Nahar and Hasanuzzaman 2009). The reduction of yield and its components under salt stress condition may be attributed to low production, expansion, senescence, and physiologically less active green foliage (Wahid et al. 1997), and thus, reduced photosynthetic rate might be a supplementary effect (Seemann and Critchley 1985). In *O. sativa* varieties, grain yield, which is the ultimate product of yield components, is greatly influenced by salinity levels. The loss of grain yield due to 150 mM salinity was 50, 38, 44, and 36 % over control for the cultivars BR11, BRRI dhan41, BRRI dhan44, and BRRI dhan46, respectively (Hasanuzzaman et al. 2009). The severe inhibitory effects of salts on fertility may be due to differential competition in carbohydrate supply between vegetative growth and constrained supply of these to the developing panicles (Murty and Murty 1982). Also reduced viability of pollen under stress condition could result in failure of seed set (Abdullah et al. 2001). Grain yield reduction of rice varieties due to salt stress is also reported earlier by Linghe and Shannon (2000) and Gain et al. (2004). As reported by Greenway and Munns (1980), after some time in 200 mM NaCl, a salt-tolerant species such as sugar beet might have a reduction of only 20 % in dry weight, a moderately tolerant species such as cotton might have a 60 % reduction, and a sensitive species such as soybean might be dead. On the other hand, a halophyte such as *Suaeda maritima* might be growing at its optimum rate (Flowers et al. 1986). In one of the recent studies on *F. vulgare*, it has been shown that yields and plant growth parameters including plant height, fresh weight yield, and biomass were affected significantly by increasing irrigation water salinities (Semiz et al. 2012).

Salt tolerance strategies in plants

Salt tolerance is the ability of plants to grow and complete their life cycle on a substrate that contains high concentrations of soluble salt. Plants that can survive on high concentrations of salt in the rhizosphere and grow well are called halophytes. Depending on their salt-tolerating capacity, halophytes are either obligate or characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50 % sea water or facultative and found in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity which enables them to cope with saline and non-saline conditions. Salt tolerance is a complex trait involving several interacting properties. There has

been increasing interest in studying the omics tools, i.e., genomics, transcriptomics, proteomics, metabolomics, etc. to identify and understand salt tolerance components and mechanisms at molecular level (Inan et al. 2004). Herein, we will briefly review roles of genomics, transcriptomics, proteomics, and metabolomics in salt stress tolerance and their possible use in enhancing salinity tolerance in plants.

Genomic level

Tolerant plants may possess some unique stress-responsive genes which are absent in susceptible plants (differences at genome structure level). Profiling at the genome level, when combined with systematic genetic analysis, promises to reveal much of the signaling networks that control stress tolerance. Munns (2005) reported genes which could increase salt tolerance fall into three main functional groups as follows: (1) those that control salt uptake and transport, (2) those that have an osmotic or protective function, and (3) those that could make a plant grow more quickly in saline soil.

Genes that control salt uptake and transport

Several *Arabidopsis* salt overly sensitive (*SOS*) mutants, defective in salt tolerance, have been characterized (Zhu et al. 1998). The *sos* mutants are specifically hypersensitive to high external Na^+ or Li^+ and also unable to grow under very low external K^+ concentrations (Zhu et al. 1998). Allelic tests indicated that the *sos* mutants define three *SOS* loci, i.e., *SOS1*, *SOS2*, and *SOS3* (Martínez-Atienza et al. 2007). The *SOS1* encodes for a plasma membrane Na^+/H^+ antiporter, responsible for the exclusion of sodium in the apoplast (Shi et al. 2000). The *SOS2* gene encodes a serine/threonine type protein kinase, which activates *SOS1* (Liu et al. 2000). The *SOS3* gene encodes an EF-hand type calcium binding protein with similarities to animal neuronal calcium sensors and the yeast calcineurin B subunit (Mahajan et al. 2008). In yeast, calcineurin plays a central role in the regulation of Na^+ and K^+ transport. Mutations in calcineurin B lead to increased sensitivity of yeast cells to growth inhibition by Na^+ and Li^+ stresses (Mendoza et al. 1994). The *SOS2* physically interacts with and is activated by *SOS3* (Halfter et al. 2000). Therefore, *SOS2* and *SOS3* define a regulatory pathway for Na^+ and K^+ homeostasis and salt tolerance in plants. Besides being regulated by *SOS2*, *SOS1* activity may also be regulated by *SOS4*. The *SOS4* catalyzes the formation of pyridoxal-5-phosphate, a cofactor that may serve as a ligand for *SOS1*, because the latter contains a putative binding sequence for this cofactor (Shi and Zhu 2002). Quan et al. (2007) reported *SOS3*-like calcium-binding protein8 (*SCaBP8*), which along with *SOS3* is required for the

activation of *SOS2*. Lin et al. (2009) further reported that *SOS2* also phosphorylates and activates downstream *SCaBP8*, but not *SOS3*. Among the three SOS loci, *SOS1* plays the greatest role in plant salt tolerance. Compared with *sos2* and *sos3* mutant plants, *sos1* mutant plants are even more sensitive to Na^+ and Li^+ stresses (Zhu 2004). Double mutant analysis indicated that *SOS1* functions in the same pathway as *SOS2* and *SOS3* (Liu et al. 2000). At the plasma membrane, a family of P-type H^+ -ATPases serves as the primary pump that generates a proton motive force for driving the active transport of other solutes; include K^+ and Na^+ (Sze et al. 1999). Much of the Na^+ that enters the cell is also compartmentalized into the vacuole through the action of vacuolar Na^+/H^+ antiporters (Apse et al. 1999). Qiu et al. (2004) reported that activity of vacuolar *NHX1* is also regulated by *SOS2*. The driving force for the vacuolar transporters is the proton motive force created by vacuolar V-type H^+ -ATPases and the H^+ -pyrophosphatase (Sze et al. 1999). Yang et al. (2009) reported an increase in salt tolerance in transgenic *Arabidopsis* over-expressing *AtNHX1*, *SOS1*, *SOS3*, *AtNHX1 + SOS3*, *SOS2 + SOS3*, or *SOS1 + SOS2 + SOS3*. *Arabidopsis* transgenic plants over-expressing SOS pathway genes showed lower Na^+ and greater K^+ accumulation, resulting in higher salinity stress tolerance (Yang et al. 2009). Kumar et al. (2009) also reported strong correlation between transcript abundance for SOS pathway related genes and salinity stress tolerance in *Brassica*. Similarly, Martínez-Atienza et al. (2007) reported that the salt tolerance of rice (*O. sativa*) was associated with greater expression of *SOS1*, *SOS2*, and *SOS3*, which correlated with its ability to exclude Na^+ from the shoot and to maintain a low cellular Na^+/K^+ ratio.

Recent sequencing of the whole genome of *Thellungiella parvula* has revealed that although the genomes of *A. thaliana* and *T. parvula* are of very similar size (140 Mb) and gene number, there are significant differences in gene copy number in certain functional categories important for stress tolerance (Dassanayake et al. 2011). A study was done to examine the role of SOS pathway in salinity stress tolerance in *Brassica* spp. The experiment was conducted in pot culture with 4 *Brassica* genotypes, i.e., CS 52 and CS 54, Varuna, and T 9 subjected to two levels of salinity treatments along with a control, viz., 1.65 (S0), 4.50 (S1), and 6.76 (S2) dS m^{-1} . Gene expression studies revealed the existence of a more efficient salt overly sensitive pathway composed of *SOS1*, *SOS2*, *SOS3*, and vacuolar Na^+/H^+ antiporter in CS 52 and CS 54 compared to Varuna and T 9. Sequence analyses of partial cDNAs showed the conserved nature of these genes and their intra and intergenic relatedness. It is thus concluded that existence of an efficient SOS pathway, resulting in higher K/Na ratio, could be one of the major factors determining salinity stress tolerance of *B. juncea* genotypes CS 52 and CS 54 (Chakraborty et al. 2012).

Genes that have osmotic or protective function

Molecules having a protective function include small organic compounds that are variously called osmolytes, osmoprotectants, or compatible solutes. These have two functional roles: at high concentrations, osmotic adjustment; and at low concentrations, an unknown protective role. Other gene products include enzymes that “mop up” free radicals and proteins that protect the formation or stability of other proteins. There are four main classes of solutes that could have an osmotic or protective role, which are as follows: the N-containing solutes such as proline and glycine betaine; sugars such as sucrose and raffinose; straight-chain polyhydric alcohols (polyols) such as mannitol and sorbitol; and cyclic polyhydric alcohols (cyclic polyols). Proteins with protective roles of unknown function include late-embryogenesis-abundant proteins (LEAs) and their close relatives with dehydrins. The osmolyte(s) and their corresponding gene(s) whose overexpression imparts salt tolerance in different plant species have been shown in Table 2.

Table 2

Osmolyte(s) and their corresponding gene(s) whose overexpression imparts salt stress tolerance in different plant species

Solute type	Natural concentration range	Overexpression studies with whole plants that resulted into increased salt tolerance				
		Solute(s)	Gene(s)	Species	Concentration	Reference
N-containing solutes such as proline, glycine, betaine, and trigonelline	1–50 mM	Proline, glycine, betaine	<i>P5CS</i> mod, <i>codA</i> , <i>P5CS</i>	Tobacco, rice	5–60 mM	Sakamoto and Alia (1998), Hong et al. (2000), Ohnishi and Murata (2006), Nounjana et al. (2012)
Trehalose	5–10 μM	Trehalose	<i>otsA</i> , <i>otsB</i> , <i>AtTPS1</i> , <i>AtTPS2</i>	Rice	300 μM	Garg et al. (2002), Baea et al. (2005)
Straight chain polyhydric such as mannitol and sorbitol	1–50 mM	Mannitol, sorbitol	<i>mt1D</i> , <i>S6PDH</i> , <i>OemaT1</i>	Wheat, tobacco, persimmon	2–60 mM	Tarczynski et al. (1993), Gao et al. (2001) Abebe et al. (2003), Conde et al. (2007)
Cyclic polyhydric alcohols such as myoinositol, ononitol, and pinitol	1–200 mM	Ononitol	<i>imt1</i>	Tobacco	35 mM	Sheveleva et al. (1997)

P5CS D¹-pyrroline-5-carboxylate synthetase, *codA* choline oxidase, *otsA* trehalose-6-phosphate synthase, *otsB* trehalose-6-phosphate phosphatase, *mt1D* mannitol-1-phosphate dehydrogenase, *S6PDH* sorbitol-6-phosphate dehydrogenase, *imt1* D-myoinositol methyltransferase, *OemaT1* mannitol-1, *AtTPS* trehalose-6-phosphate synthase

Genes that control cell and tissue growth rates

Candidate genes controlling growth are probably involved in signaling pathways that start with a sensor and involve hormones, transcription factors, protein kinases, protein phosphatase, and other signaling molecules such as calmodulin binding proteins. It is highly likely that such genes are common to drought stress (reviewed by Chaves et al. 2003) and are common to other

stresses, such as cold, and soil conditions that reduce growth such as soil hardness caused by compaction or sodicity. Many are induced by treatment with abscisic acid (ABA). The sensor may be a metabolite that changes in concentration or a membrane protein that changes in configuration, as the cell shrinks in response to a salt, drought or cold stress, or a long-distance signal moving from roots to shoots in the transpiration stream.

Transcriptomic level

Tolerant plants reveal altered regulation of gene expression of important stress-responsive genes than susceptible plants (qualitative and quantitative differences at gene expression level). It reveals the altered regulation of stress responsive genes. A transcriptomic study done by Kumari et al. (2009) on a salt-sensitive rice line IR64 and a salt-tolerant rice Pokkali has led to the identification of a set of salinity-responsive genes including GST, LEA, V-ATPase, OSAP1 zinc finger protein, and transcription factor HB1B displaying a higher expression in Pokkali than in IR64 and possibly contributing to a higher salinity tolerance of Pokkali. The transcriptomic section has been divided in the following subheadings:

Transcription factors

A transcription factor (sometimes called a sequence-specific DNA-binding factor) is a protein that binds to specific DNA sequences, thereby, controlling the flow (or transcription) of genetic information from DNA to messenger RNA and is responsible for the expression of stress-activated genes associated with plant tolerance and adaptation. Many transcription factors that share the homologous DNA binding domain and are classified in families based on their DNA-binding domains, such as the MYB-like proteins (containing helix-turn-helix motifs), the MADS domain proteins, the homeobox proteins, the bZip (basic region leucine zipper) proteins, or the zinc finger protein. A basic helix-loop-helix (bHLH) encoding gene, *OrbHLH2*, functions as a transcription factor and positively regulates salt-stress signals and overexpression of *OrbHLH2* in *Arabidopsis* conferred increased tolerance to salt and osmotic stress (Zhou et al. 2009). The bZIP transcription factor controls the expression of stress-related genes (Djamei et al. 2007), including transcription factor *MYB44* (Pitzschke et al. 2009). Moreover, the *MYB44* gene product itself can serve as target for mitogen-activated protein kinase (MPK) 3 phosphorylation suggesting a sophisticated multi-level control mechanism (Persak and Pitzschke 2013). The *MYB44* overexpression confers abiotic stress tolerance in a phosphorylation-dependent manner. One of the stress related zinc finger proteins called as ZAT7

from *A. thaliana* caused an increased expression of genes responsible for salt tolerance (Ciftci-Yilmaz et al. 2007). Another transcription factor, *ONAC063* gene that was localized in the nucleus, was induced by high-salinity in rice roots (Yokotani et al. 2009). The seeds of *ONAC063*-expressing transgenic *Arabidopsis* showed enhanced tolerance to high-salinity and osmotic pressure indicating a possible role of *ONAC063* in eliciting responses to high-salinity stress. Basic helix-loop-helix transcription factor from wild rice (*OrbHLH2*) has recently been shown to improve tolerance to salt- and osmotic-stress in *Arabidopsis* (Zhou et al. 2009).

MAP kinases

Mitogen-activated protein kinase (MAPK) cascades are conserved eukaryotic signaling modules which play key regulatory roles in development as well as in numerous stress responses. Acting early after stress perception, they serve for both amplification and transduction of the stress information. A well-studied stress-related MAPK cascade is the HOG1 pathway, which regulates the high-osmolarity response in yeast (Zi et al. 2010). Similarly, stress-related MAPK cascades have been discovered in animals (Ballif and Blenis 2001; Kyriakis and Avruch 2012) and plants (Rodriguez et al. 2010). MPK cascades consist of three sequential components, MPK kinase kinase, MPKkinase (MKK), and MPK. Various combinations of MPK cascades mediate plant tolerance to NaCl and play roles in cell wall biosynthesis and cell growth and differentiation (Colcombet and Hirt 2008). Irrespective of the organism, signaling involves a phosphor-relay mechanism: a MAPKKK activates its downstream MAPKK which in turn activates a target MAPK. Finally, MAPKs regulate the properties of substrate proteins through phosphorylation at serine or threonine residues adjacent to a proline (S/T-P). A kinase interaction motif (R/K-x(2–6)-I/LxI/L) found in a number of plant MAPK targets has been shown to assist substrate binding (Schweighofer et al. 2007). Among the 10 MAPKKs and 20 MAPKs in *Arabidopsis*, MKK4/MKK5 and their direct substrates, MPK3/MPK6 in particular, are strongly associated with stress signaling. They are activated by various biotic and abiotic stimuli (Colcombet and Hirt 2008; Pitzschke et al. 2009; Rodriguez et al. 2010; Samajova et al. 2013). Both MKK4/MKK5 and MPK3/MPK6 are pairs of closely related proteins, which have highly, but not entirely, overlapping functions. But overexpression of *MKK4* is accompanied by MPK3/MPK6 hyper activation which enhances stress tolerance (Kim et al. 2011). The MAPKs may further regulate plant cell shapes by interacting with or regulating cortical microtubules, as was shown for MPK4 (Beck et al. 2010; Beck et al. 2011), MPK6 (Müller et al. 2010), and MPK12/MPK18 (Walia et al. 2009). Recently, Campo et al. (2014) reported that overexpression of *OsCPK4* enhanced salt tolerance in rice by preventing lipid peroxidation in membranes.

MicroRNAs

MicroRNAs are known as ubiquitous regulators of gene expression in eukaryotic organisms. In plants, functional analysis has demonstrated that several miRNAs play vital roles in plant resistance to abiotic and biotic stress (Sunkar and Zhu 2004; Navarro et al. 2006). Various studies on *Arabidopsis*, rice, and other plants have revealed an important role for miRNAs in drought and salt responses. Recently in *Arabidopsis*, several differentially regulated miRNAs have been identified in salt-stressed tissues. In response to salt stress, miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394, miR396, and miR397 were upregulated, while the miR398 was downregulated, and thus, establishing a role for miRNAs in the adaptive response to salt stress (Liu et al. 2008). Upregulation of miRS1 and miR159.2 in response to salt stress was observed in *Phaseolous vulgaris* (Arenas-Huertero et al. 2009). The expression of miR530a, miR1445, miR1446a-e, miR1447, and miR1711-n was increased; whereas, miR482.2 and miR1450 were decreased during salt stress in *Phaseolus trichocarpa* (Lu et al. 2008). Further, two members of miR169 family viz. miR169g and miR169n showed enhanced expression during salinity. Interestingly, a cis-acting ABA-responsive element was identified in the upstream region of miR169n, which gave an indication that miR169n may be regulated by stress hormone ABA. In a study between salt tolerant maize genotype NC286 and salt sensitive maize genotypes Huangzao4, it was demonstrated that miR156, miR164, miR167, and miR396 families were downregulated, while miR162, miR168, miR395, and miR474 families were upregulated in salt-stressed maize roots. The study also proposed a gene model that regulates the abiotic stresses and gene networks coping with the stress (Ding et al. 2009). Soybean miRNAs associated with salt stress responses have been identified and analyzed by utilizing the next generation sequencing technology and bioinformatics tools. One hundred and thirty-three conserved miRNAs representing 95 miRNA families were differentially expressed in soybeans under different stress treatments along with 50 miRNAs differently expressed under salt stress (Li et al. 2011a). The MiR159 and 319 were upregulated following saline treatment in artichoke tissues (De Paola et al. 2012).

Proteomic level

Proteins involved in stress response reveal an altered activity in tolerant plants than in susceptible ones (differences in protein structure and activity level). Several studies on the molecular mechanisms regulating salt stress response in plants have focused on changes in transcription (Brumós et al. 2009). However, phenotypic performance also depends on protein expression, as well

as on their post-translational modifications that cannot be identified by simply analyzing transcription. Therefore, proteomic analysis may provide a powerful molecular tool to complement genomic and transcriptomic analysis. A mere protein differential abundance does not give much information on protein function under salinity and therefore validation of comparative proteomics should be done by protein functional analysis. Therefore, other approaches (e.g., post-translational modifications, protein-protein interactions, tissue and subcellular localization, and phenotype influence on silencing or overexpressing of a gene encoding a protein of interest) have to be employed to unravel the role of the proteins in acquisition and development of salinity tolerance in plants. Several functional groups of proteins affected by salt stress including proteins involved in signaling, ion transport, energy metabolism (photosynthesis, ATP production, respiration), carbohydrate, protein and lipid metabolism, metabolism of osmolytes and phytohormones, stress-related proteins (oxidative stress-ROS scavenging enzymes, pathogenesis related proteins, osmotic stress-related proteins-osmotin), cytoskeleton and cytoskeleton-associated proteins, enzymes involved in secondary metabolism (biosynthesis of lignin, degradation of cyanate), and others (Kosová et al. 2013). Below, the main protein functional groups affected by salt stress are discussed in detail.

With the help of 2DE experiments, some Ca binding proteins activated by salinity stress have been detected including plasma membrane protein annexin (Pang et al. 2010) and calmodulin (Cheng et al. 2009). These proteins were observed to mediate osmotic stress and ABA signal transduction (Lee et al. 2004a, b) and their levels were increased in salt-exposed shoots of *Salicornia europaea*, one of the most tolerant salt plant species (Wang et al. 2009) and in the tobacco salt-stressed roots (Manaa et al. 2011). Other differentially abundant signaling proteins belonging to the Rab family of guanosine triphosphate-binding proteins (GTPase) are also involved in stress signal transduction *via* regulation of endocytosis and vesicle trafficking (Wang et al. 2008a; Pang et al. 2010). A gene encoding a small GTP related to the *Rab2* gene family of GTPases was induced by salt stress in *Lolium temulentum* (Dombrowski et al. 2008).

In salt-treated rice root cells, a new salt-responding leucine-rich-repeat type receptor-like protein kinase OsRPK1 was identified by Cheng et al. (2009). An increased relative abundance of 14-3-3 like proteins which are known to interact with MAPK kinase cascade to regulate the activity of plasma membrane H⁺-ATPases and to contribute to a maintenance of intracellular ion homeostasis has been found in *Physcomitrella patens* gametophyte (Wang et al. 2008b), common wheat Jinan 177 and *T. aestivum/Thinopyrum ponticum* introgression hybrid (Wang et al. 2008a), in maize root (Zörb et al. 2010), and grass pea leaves (Chattopadhyay et al. 2011).

Changes in gene expression and an enhanced risk of protein damage induce alterations in DNA remodeling, transcription, and protein metabolism which includes protein biosynthesis as well as protein degradation. Regarding the DNA remodeling, enzymes such as DNA topoisomerase and DNA helicase have been found indicating an altered and enhanced gene expression activity. And with the changes in gene expression (DNA remodeling and transcription processes), changes in abundance of several proteins involved in protein biosynthesis have been detected which in turn lead to the increased relative abundance of several translation initiation and elongation factors (e.g., eukaryotic initiation factor eIF3A, eukaryotic elongation factors eEF1B alpha 2 subunit, and eEF2 in salt-treated *A. thaliana* (Pang et al. 2010) as well as changes in several ribosomal proteins (40S ribosomal proteins S2, S7, S24, S29; 60S ribosomal proteins L5, L12, L13A, L29, L39; Kim et al. 2005; Chitteti and Peng 2007; Vincent et al. 2007; Pang et al. 2010). An active stress acclimation and salinity tolerance processes are conferred by an enhanced biosynthesis of several novel proteins. In salt-tolerant plants an enhanced protein biosynthesis is reflected by an enhanced nitrogen assimilation and amino acid biosynthesis which confers to the enhanced abundance of glutamate ammonia ligase as it plays an important role in nitrogen assimilation and amino acid biosynthesis in *Sorghum bicolor* (Kumar Swami et al. 2011) and an enhanced abundance of several aminotransferases, namely glutamine synthetase (GS), was also observed in salt-tolerant plants such as *Salicornia europaea* (Wang et al. 2009) and *Thellungiella salsuginea* (Pang et al. 2010). In contrast, in salt-sensitive plants such as potato, a decreased relative abundance of some proteins involved in protein and amino acid biosynthesis such as an mRNA binding protein and GS has been observed (Aghaei et al. 2008). Similarly, in salt-treated *Arabidopsis* cell culture, a decreased relative abundance of several proteosynthesis-related proteins such as eukaryotic translation initiation factor eIF-4E2, putative elongation factor EF2 or tRNA synthase class II was observed (Ndimba et al. 2005) indicating a suppression of protein biosynthesis upon salt stress. Considering protein degradation, increased relative abundance of proteosome subunits, e.g., proteosome subunit alpha type 6 in *Suaeda aegyptiaca* (Askari et al. 2006), putative alpha1 subunit of 20S proteosome in rice panicles (Dooki et al. 2006) or 26S proteosomal subunit in foxtail millet (Veeranagamallaiah et al. 2008) and *Salicornia europaea* (Wang et al. 2009) indicates an enhanced protein degradation upon salt stress. Increased relative abundance of FtsH-like protein, an ATP-dependent metalloprotease involved in degradation of D1 core component of PSII, indicates an enhanced damage of photosystem core proteins upon salinity (Zörb et al. 2009).

Salinity stress reveals profound impacts on plant energy metabolism. Due to osmotic stress, there is enhanced stomatal closure and a reduced CO₂ availability; CO₂ assimilation decreased in most of the plants. A reduced CO₂ assimilation rate is reflected by a decreased abundance of Rubisco large and small subunits, OEE proteins (components of oxygen evolving complex), carbonic

anhydrase, and Rubisco activase and an enhanced degradation of Rubisco subunits observed in several glycophytic plants and crops exposed to salt (Aghaei et al. 2008; Pang et al. 2010; Sobhanian et al. 2010a; Bandehagh et al. 2011; Chattopadhyay et al. 2011). Besides activation of Rubisco, Rubisco activase also reveals a chaperone function under stress (Kim et al. 2005; Fatehi et al. 2012). Similarly, an increased relative abundance of OEE2 protein was found in salt-treated barley (Rasoulnia et al. 2011; Fatehi et al. 2012), possibly as a compensation for stress-induced damage of PSII core. An enhanced abundance of ferredoxin NADPH reductase, 23 kDa polypeptide of PSII and the FtsH-like protein has been observed in salt-exposed maize chloroplast fraction which may be due to adverse impacts of Na⁺ on photosynthetic electron transport chain (Zörb et al. 2009). Other salt-increased proteins with protective functions on photosystems include CP47 protein revealing protective effects on D1 protein in RC PSII and PSI subunit IV protein (Veeranagamallaiah et al. 2008; Sengupta and Majumder 2009) and in one of the study on *Porteresia* enhanced accumulation of CP47 has been observed under salt stress (Sengupta and Majumder 2009). Enzymes associated with carbohydrate metabolism (Calvin cycle, glycolysis) have been found to increase under salt stress. As an example, fructose-1,6-bisphosphatase (FBPase) and fructose-1,6-bisphosphatase aldolase (FBP aldolase) can be given (Kim et al. 2005). The FBPase catalyses hydrolysis of fructose-1,6-bisphosphate to fructose-6-phosphate and FBP aldolase catalyses conversion (splitting) of fructose-1,6-bisphosphate into glyceraldehyde-3-phosphate and dihydroxyacetone phosphate. Increased relative abundance of FBP aldolase together with other glycolytic enzymes and enzymes involved in ethanolic fermentation and glycolate metabolism in rice seedlings indicates an increased relative abundance of anaerobic metabolism under salt stress (Abbasi and Komatsu 2004). An increased relative abundance of alcohol dehydrogenase has been found in hypocotyls of salt-stressed soybean (Sobhanian et al. 2010a) and grasspea leaves (Chattopadhyay et al. 2011). Moreover, it has been hypothesized that FBP aldolase could play a role in salt ion vacuolar compartmentation since it can directly physically interact with tonoplast H⁺-ATPase and activates its transport function (Barkla et al. 2009; Tada and Kashimura 2009). It can thus be concluded that in glycophytes, photosynthesis (CO₂ assimilation) is decreased by salt stress. However, in some halophytic plants, maintenance or even an increased net photosynthesis rate under salt stress has been found or in *Porteresia coarctata* leaves (Sengupta and Majumder 2009).

Another strategy which seems to be suitable under conditions of restricted CO₂ (stomata closure) and water availability lies in C₄ photosynthesis. An increased abundance of NAD-malic enzyme has been detected in *Aeluropus lagopoides*, a halophytic C₄ plant from *Poaceae* family, while a decrease in Calvin cycle enzymes was observed (Sobhanian et al. 2010b). In response to salt stress, an increased relative abundance of several proteins involved in metabolic processes leading to energy production (energy

release) such as glycolysis, tricarboxylic (TCA) acid cycle, photorespiratory pathway and pentose phosphate pathway (PPP) has been found. In a comparative proteomic study of salt-treated *A. thaliana* and *T. salsuginea*, a higher relative abundance of respiration-related enzymes was found in *Arabidopsis* than in *Thellungiella* (Pang et al. 2010). Plant responses to salinity pose enhanced demands on energy production. Therefore, an enhanced abundance of several subunits of ATP synthase, namely subunit β , involved in ATP biosynthesis has been found in several tolerant salt-treated plants (Kim et al. 2005; Veeranagamallaiah et al. 2008; Geissler et al. 2010; Pang et al. 2010; Li et al. 2011a). In addition, an increased relative abundance of enzymes involved in ATP biosynthesis (adenylate kinase ADK) and energy salvage (nucleoside diphosphate kinase 1 (NDPK1) involved in interconversion between ATP and CTP, GTP, and UTP) have been observed in salt-tolerant plants such as *S. salsa* (Li et al. 2011b) in pea plants (Kav et al. 2004) and wheat (Jacoby et al. 2010). In *Arabidopsis*, NDPK interacts with MAPK-mediated H_2O_2 signaling, downregulates the production of ROS, and enhances stress tolerance (Moon et al. 2003).

With the consistent alterations in energy metabolism, there is an increased risk of oxidative damage in salt-treated plants that leads to the formation of ROS and enhanced ROS formation results in an increased relative abundance of several ROS scavenging enzymes such as catalase (CAT), superoxide dismutase (SOD), enzymes of ascorbate-glutathione cycle: ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR; Kav et al. 2004; Chen et al. 2009; Sugimoto and Takeda 2009), cytochrome P450 monooxygenase, thioredoxin *h* (Trx *h*), glutathione-*S*-transferase (GST), etc., and other proteins involved in maintenance of plant redox status-protein disulfide isomerase (Kim et al. 2005; Dooki et al. 2006; Aghaei et al. 2008; Wang et al. 2008a; Geissler et al. 2010; Pang et al. 2010; Kumar Swami et al. 2011). Besides activation of ROS scavenging enzymes, other responses could be observed in salt-treated plants. An increased abundance of tocopherol cyclase, a crucial enzyme in the biosynthesis of α -tocopherol, an important compound in plant non-enzymatic ROS scavenging mechanisms, has been found in Chinese halophytic plant *Puccinellia tenuiflora* (Yu et al. 2011). An increased abundance of mitochondrial alternative oxidase (AOX), an enzyme involved in so-called “cyanide-resistant respiration,” i.e., respiration without utilization of cytochromes leading to a reduced ROS formation, has been observed in salt-treated wheat mitochondria (Jacoby et al. 2010).

It is also known that free metal ions could act as catalysers of ROS formation. Therefore, responses leading to elimination of free metal ions were observed in salt-stressed plants. In salt-exposed barley roots, a decrease in IDI2, IDS2, and IDS3 proteins

has been observed (Witzel et al. 2009). The reduced relative abundance of IDI2, IDS2, and IDS3 indicates a decrease in Fe consumption which may reflect the avoidance of metal ion-induced oxidative stress. Consistent with the aim to maintain low levels of free intracellular Fe, an increased abundance of ferritin, an Fe-binding protein, was found in salt-treated rice (Kim et al. 2005), *Arabidopsis* cell culture (Ndimba et al. 2005) and tomato (Chen et al. 2009) seedlings, and accumulation of triplicated transferrin-like protein was detected in *Dunaliella salina* (Liska et al. 2004). An elevated abundance of magnesium chelatase, an enzyme involved in incorporating magnesium into chlorophyll structure which catalyses the first unique step of the chlorophyll biosynthetic pathway, has been found in salt-treated barley (Rasoulnia et al. 2011). Salt stress also causes an augmentation of several proteins with protective functions such as chaperones from HSP90 family in tomato roots (Manaa et al. 2011) and HSP 70 family, Hsc70 (heat-shock cognate) proteins in *A. thaliana* (Pang et al. 2010) and *P. patens* (Wang et al. 2008a), DnaK protein, and others in salt-treated rice seedlings (Kim et al. 2005; Chitteti and Peng 2007) or *Arabidopsis* cell culture (Ndimba et al. 2005). Increased relative abundance of several small HSPs (mitochondrial small HSP, chloroplast HSP, 17.8 kDa class I small HSP, HSP20) was found in salt-treated tomato hypocotyls (Chen et al. 2009) and *Aster tripolium* leaves (Geissler et al. 2010). Increased relative abundance of STI1 protein, a stress-responsive protein with two heat shock chaperonin-binding motifs and three tetratricopeptide repeats (TPR) in salt-treated rice panicles (Dooki et al. 2006) points toward a large regulatory network affected by salt stress since TPR-containing proteins have been reported as being involved in myriads of processes including HSP90 signaling, gibberellin signaling and protein mitochondrial transport.

Other stress-responsive proteins include germin-like proteins (GLPs) which play an important role in plant embryogenesis. Some GLPs display oxalate oxidase and SOD activities. Increased relative abundance of germin-like proteins was observed under several abiotic and biotic stress conditions, for example in salt-stressed barley leaves (Fatehi et al. 2012) and *Arabidopsis* roots (Jiang et al. 2007). Another interesting protein group induced by salinity is lectins which are known as being involved in protein-saccharide interactions and stress signaling. Small lectins with a jacalin domain have been proposed to function in plant defense mechanisms (Zhang et al. 2000). An increased relative abundance of a jacalin lectin family protein was observed in salt-treated *A. thaliana* leaves (Pang et al. 2010). Other stress-protective proteins, such as osmotin and osmotin-like proteins, are associated with a plant adjustment to an enhanced osmotic stress. Increase in osmotin and osmotin-like proteins has been found in various salt-treated plants ranging from a salt-tolerant cultivar of potato (Aghaei et al. 2008) and hypocotyls of tomato (Chen et al. 2009) to roots of a halophytic mangrove plant *Bruguiera gymnorhiza* (Tada and Kashimura 2009).

Metabolomics

Metabolomics is an important functional genomics tool for understanding plant response to salt stress (Lu et al. 2013). The high-throughput omics such as metabolomics improved understanding of salt stress-induced changes in gene-protein-metabolite (Urano et al. 2010). Currently, this has been applied in understanding multiple physiological processes in plants in combination with other platforms such as transcript profiling and proteomics (Wu et al. 2013). Major approaches currently being used in plant metabolomics are metabolic fingerprinting, metabolite profiling, and targeted analysis. In recent years, metabolomics analysis is being widely used to investigate abiotic stresses including salinity stress tolerance of plants (Alvarez et al. 2008; Shulaev et al. 2008; Renberg et al. 2010). Herein, we described the role of metabolomics in salt stress tolerance in plants under following subheadings:

Osmolyte metabolism

A decreased osmotic potential of water containing high concentrations of dissolved salt ions poses an enhanced osmotic stress on plant cells. Thus, to overcome the stress, plant cells achieve osmotic adjustment by accumulation of inorganic salt ions that includes hydrophilic compounds, called osmolytes, and hydrophilic proteins with osmoprotective function. In salt-treated plants, changes in metabolism of several osmolytes, namely proline and glycine betaine (GB), have been found. An increased level of enzymes involved in proline biosynthesis, and in contrast, a decreased level of enzyme catalyzing proline hydrolysis have been found in *Thellungiella* under salt stress (Pang et al. 2010). An increased relative abundance of enzymes involved in GB biosynthesis such as *S*-adenosylmethioninesynthetase (SAMS), choline monooxygenase, and betaine aldehyde dehydrogenase has been found in salt-treated *Suaeda aegyptiaca* (Askari et al. 2006) and foxtail millet (Veeranagamallaiah et al. 2008). Hydrophilic proteins with osmoprotective function (e.g., proteins from LEA superfamily including dehydrins) have been found to be elevated (reviewed in Battaglia et al. 2008; Hundertmark and Hinch 2008; Kosová et al. 2010). As examples of salt-inducible LEA proteins, dehydrin TAS14 in tomato (Godoy et al. 1994), several dehydrins, and LEA3 proteins in salt-tolerant Indica rice cultivars Pokkali and Nona Bokra have been reported (Moons et al. 1995). Recently, Wu et al. (2013) reported that salt stress elevated concentrations of several compatible solutes—proline, glycine, alanine, mannitol, inositol, raffinose, glucose, fructose-6-phosphate, etc. in barley which impart salt tolerance.

Phytohormone metabolism

Changes in abundance of several enzymes involved in phytohormone metabolism such as jasmonic acid (JA) biosynthesis (allene oxide cyclase, AOC; lipoxygenase, LOX), gibberellin (GA) biosynthesis (DWARF3), ethylene biosynthesis (SAMS), and ABA biosynthesis (*9-cis*-epoxycarotenoid dioxygenase; NCED) have been detected in salt-treated plants. Increased relative abundance of ABA biosynthesis (increase in NCED level) found in *T. salsuginea* (Taji et al. 2004) corresponds with enhanced ABA levels observed in salt-treated plants and with an increased expression of several early (ABA-dependent transcription factors) and delayed (genes induced by ABA-dependent transcription factors, e.g., *Lea/Rab* genes) ABA-responsive genes. An enhanced induction of ethylene receptor ETR1 was found in common wheat cv. Jinan under salinity (Peng et al. 2009). Activation of JA biosynthesis (increase in AOC and LOX levels) in salt-treated *A. thaliana* indicates an increased relative abundance of JA-induced signaling under salt stress has also been reported (Pang et al. 2010).

Lipid metabolism

Changes observed in lipid metabolism in salt-treated plants can be associated with adverse effects of salt stress, namely its osmotic component, on membrane integrity and function. In a comparative proteomic study of salt-treated *A. thaliana* and *T. salsuginea* (Pang et al. 2010), an augmented abundance of 3-ketoacyl-acyl carrier protein synthase I and phospholipase/carboxyesterase family protein has been found in salt-treated *A. thaliana*. In *T. salsuginea*, an elevated level of a putative long-chain-fatty-acid-CoA ligase involved in fatty acid synthesis and a declined level of a putative glycerophosphodiester phosphodiesterase involved in lipid degradation was found (Pang et al. 2010). Increased relative abundance of dihydrolipoamide dehydrogenase and enoyl-ACP reductase has been found in salt-treated rice panicles (Dooki et al. 2006). The changes observed in lipid metabolism in salinity-exposed plants indicate profound changes in cell membrane integrity, composition, and function under stress. A short-term decreased relative abundance of monogalactosyl diacylglycerol synthase, an enzyme involved in biosynthesis of galactosylglycerolipids (monogalactosyl diacylglycerol, digalactosyl diacylglycerol), the major components of chloroplast inner envelope and thylakoid system, observed in salt-treated maize chloroplasts (Zörb et al. 2009), and an increased relative abundance of UDP-sulfoquinovose synthase involved in biosynthesis of thylakoid membrane sulfolipids observed in creeping bent grass (Xu et al. 2010) indicate profound changes in chloroplast membrane structure and composition in response to salt and osmotic stress. Changes in lipid-metabolism associated lipid transfer proteins and temperature-induced lipocalins have been observed in apoplastic fluid of tobacco cells (Dani et al. 2005) and tomato radicals (Chen et al. 2009), respectively, subjected to salinity stress. Lipid transfer proteins are known to be involved

in plant response to pathogens (Garcia-Olmedo et al. 1995) and lipocalins are known to display a protective role against photooxidative damage (Bugos et al. 1998).

Conclusion and future perspectives

Crop productivity is severely affected by salinity stress. This occurs directly due to the impact of salinity on photosynthesis, respiration, nutrient assimilation, hormonal imbalance, etc. The indirect adverse effect of salinity is enhanced generation of reactive oxygen species in stressed plant which subsequently cause damage to macromolecules such as lipids, proteins, and nucleic acids, and thus, constrain crop productivity. Therefore, to engineer more salt-tolerant plants, it is important to find out the key components of the plant salt-tolerance network. Recently, genomics, transcriptomics, proteomics, and metabolomics have been successfully applied and given exciting outcome to unravel different components of salt tolerance in plants. These components include various genes (*SOS* signaling-network), transcription factors (HLH, MYB, etc.), and proteins and metabolites (osmolytes, phytohormones, lipids, etc.) which may be used to engineer plants for their increased salt tolerance. This multidisciplinary approach will be highly helpful in increasing plant as well as crop productivity to meet out increasing demand of food for ever increasing population. Probable routes of salt stress toxicity and its various tolerance strategies in plants are depicted in Fig. 4.

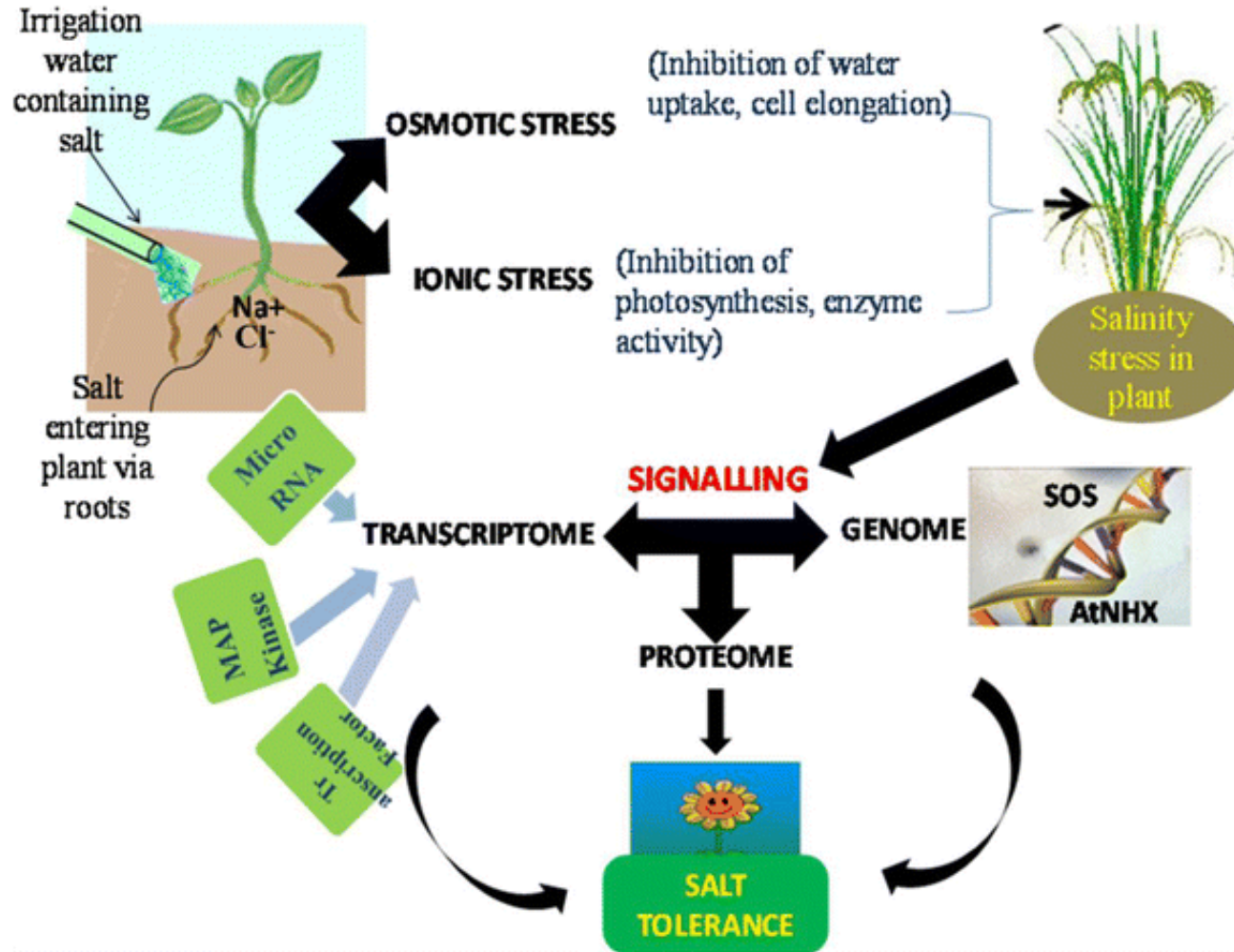


Fig. 4

Schematic diagram is showing routes of salt stress toxicity and its various tolerance strategies in plants. In salt tolerance strategies, putative roles and action of genes, transcription factors, MAP kinases, microRNAs, and metabolites are shown

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