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Biochemical and Molecular Basis of Salinity Stress Tolerance in Plants: Role of Salicylic Acid

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ABSTRACT

Environmental stresses come in many forms and the ability to withstand these stresses is one of the most important factors that decide the distribution of plant species in an area. These stresses affect several physiological, biochemical and molecular processes in plants and limit plant productivity. The study of abiotic stresses especially salinity in plants has advanced significantly in recent years, however the majority of experiments testing the response of plants to salt stress have focused on chemical treatment applied to plants under controlled conditions. Thus development of methods for inducing stress tolerance in plants is vital and would be a major focus of research in adverse environmental conditions. More recently, some of the endogenous growth regulators like abscisic acid, jasmonic acid and salicylic acid (SA) have been implicated in imparting stress tolerance in plants. SA has appeared as a signaling molecule modulating plant response to biotic and abiotic stresses. The established effects of SA on photosynthetic activity, nitrate assimilation and regulation of ROS in plants, give an indication that SA might possess defensive function probably induction of some stress responsive proteins in plants under saline conditions . It also counteracts the deleterious effects of salt on biochemical changes like decreasing MDA content (a product of lipid peroxidation), and free proline content. Thus studies suggest that exogenous application of salicylic acid in plants may bring some potential practical utilization. For example, manipulating the tissue level of SA in plants may be a promising area for the importance of biotechnology to crop protection and high yield. The main objective of this article was to develop new concept about the role of salicylic acid in growth characteristics, metabolic homeostasis, osmoregulation, ROS regulation, gene induction and signaling of various metabolic pathways in plants.

Keywords: adaptation, antioxidant enzymes, compatible solutes, reactive oxygen species, salicylic acid

CONTENTS

INTRODUCTION

Plant growth is greatly affected by a combination of environmental stresses such as extreme temperatures, drought or high salinity. From an agricultural perspective, such stresses are among the most significant factors responsible for substantial losses in crop productivity. Most stresses have in common their effect on plant water status. These environmental stresses often impair the availability of water for its biological functions like its role as a solvent, transpirant, electron donor; transport medium, etc. (Zhu 2002; Sairam and Tyagi 2004). Salinity is one of the major stresses responsible for changes in metabolic activity of plants. Soil salinization is continuously reducing the arable land for conventional agriculture and resulting in severe agricultural losses (Parida and Das 2005). Plants have evolved several adaptive mechanisms to cope with the salinity in their environment, but the understanding of these mechanisms still remains incomplete. Thus development of methods for inducing stress tolerance in plants is vital and is a major focus of research over many decades.

Some endogenous growth regulators like ABA (abscisic acid), JA (jasmonic acid) and SA (salicylic acid) have been implicated in imparting stress tolerance in plants (Overmyer *et al*. 2003; Mittler *et al*. 2004; Gunes *et al*. 2007; Gautam and Singh 2009). SA is a well known naturally occurring signaling molecule that is involved in establishing and signaling a defense response against various biotic and abiotic stresses. Investigations show the role of SA in modulating plant responses to a wide range of oxidative stresses (Singh *et al.* 2008). Reports prove that induction of multiple stress tolerance in plants by exogenous SA application may have a

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significant practical application in agriculture, horticulture and forestry. The established effects of SA on stomatal function, chlorophyll content, transpiration rate and respiratory pathways raise the assumption that SA might possess another physiological function, most probably involved in regulation of some photosynthetic reactions and other growth regulatory mechanisms under salinity stress in plants (Borsani *et al.* 2001; Senaratna *et al.* 2003; Gunes *et al.* 2007; Gautam and Singh 2009).

Thus studies suggest that exogenous application of SA in plants may bring some potential practical utilization. For example, manipulating the tissue level of SA in plants may be a promising area for the importance of biotechnology to crop protection and high yield. Increase in endogenous SA may be achieved via enhancing transcription and translation of the genes for SA biosynthesis or by blocking the expression of genes involved in SA metabolism. The main objective of this article was to develop a new concept about the role of salicylic acid in growth regulation, gene induction and signal transduction pathways in plants grown under saline environment. In the present review, information is presented on SA induced protein kinases (SIPK), osmotolerance, antioxidative system, ABA signaling and ion homeostasis in plants.

SALINITY STRESS

Effect of salinity is more harmful during early stages of germination and seedling growth, which ultimately results in decreased crop yield (More *et al.* 2004; Verma *et al.* 2005). It leads to both ionic and osmotic stresses. Most commonly, soil salinity affects plant growth and development by way of injurious effects of toxic Na^+ and Cl^- ions and to some extent Cl^- and SO_4^{2-} of Mg^{2+} and nutrient imbalance caused by these ions (Sairam and Tyagi 2004). High salt concentrations (most commonly NaCl) in the soil lead to a decrease in water potential, thus affecting water availability (Hasegawa *et al.* 2000). This altered water status causes initial growth reduction followed by inhibition of cell division and expansion, reactive oxygen species, metabolic toxicity and inhibition of photosynthesis and nitrate assimilation.

Salt movement through plants

Movement of salt into roots and to shoots is a product of the transpirational flux required to maintain the water status of the plant because, unregulated transpiration can result in toxic levels of ion accumulation in the aerial parts of the plant (Hasegawa *et al.* 2000). An immediate response to salinity, which mitigates ion flux to the shoot, is stomatal closure. However, due to water potential difference between the atmosphere and leaf cells, and the need for carbon fixation, this is an untenable long-term strategy of salt tolerance (Yeo 1998). To protect actively growing and metabolizing cells, plant regulates ion movement into tissues. One mode by which plants control salt flux to the shoot is the entry of ions into the xylem stream, which may depend on symplastic ion transport through the epidermal and cortical cells, contributes to a reduction in Na^+ that is delivered to the xylem. However, at the endodermis, radial movement of solutes must be via a symplastic pathway, as the Casparian strip constitutes a physical barrier to apoplastic transport (Flowers and Yeo 1992).

The accumulation of large quantities of ions in mature and old leaves, which then dehisce, has often been observed under salt stress (Munns and Tester 2008). In a function as ion sinks, old leaves may restrict ion deposition into meristematic and actively growing and photosynthesizing cells. An alternative possibility is that cellular ion discrimination is a natural consequence of transpirational and expansive growth fluxes, cell morphology, and degree of intracellular connection. Meristematic cells, which are not directly connected to the vasculature, are less exposed to ions delivered through the transpiration stream, and their small vacuolar space is not conducive to ion storage. *De facto*, the solute content of tissues containing cells with little vacuolation (e.g. meristematic regions) is predominated by organic osmolytes and in tissues with highly vacuolated cells by ions (Binzel *et al.* 1988).

Ion homeostasis and vacuolar compartmentation

Ion homeostasis in saline environments is dependent on *trans*-membrane transport proteins that mediate ion fluxes, including H^+ translocating ATPases and pyrophosphatases, Ca^{2+}-ATPases, secondary active transporters, and channels (Sze *et al.* 1999). Actually, salt stress is sensed through SOS pathway, which comprises of three key components: SOS3, acting as Ca^{2+} sensor (Liu and Zhu 1998); SOS2, a serine/threonine protein kinase (Liu *et al.* 2000); and SOS1, a plasma membrane Na^+/H^+ antiporter (Shi *et al.* 2000). Compartmentalization of Na^+ into the vacuoles or its efflux across the plasma membrane are mediated by the expression and activity of Na^+/H^+ antiporters as well as of V-type H^+-ATPase and H^+-PPase (Chinnusamy *et al.* 2005).

The SOS1 protein has transmembrane domains to sense Na^+ and is supposed to exist in the cytoplasm (Shi *et al.* 2000; Zhu 2003; Zhang *et al.* 2004; Shabala *et al.* 2005). Thus, Na^+/H^+ antiport activity of SOS1 results in efflux of excess Na^+ ions and thus contributes to Na^+ ion homeostasis (Liu and Zhu 1998; Halfter *et al.* 2000; Ishitani *et al.* 2000; Liu *et al.* 2000; Quintero *et al.* 2002). SOS1 has also been reported to protect plasmamembrane K^+ transport during salinity stress (Shabala *et al.* 2005). SOS3/SOS2 protein kinase complex appears to down-regulate the activity of AtHKT1 (low-affinity Na^+ transporter) under salt stress (Mahajan and Tuteja 2005), which mediates Na^+ entry into the root cells of *Arabidopsis* (Uozumi *et al.* 2000; Zhu 2002). SOS2 is shown to interact with vacuolar Na^+/H^+ antiporter (NHX) influencing its Na^+/H^+ exchange activity, resulting in sequestration of excess Na^+ ions into vacuolar compartment and thus further contributing ion homeostasis (Qiu *et al.* 2002; Munns and Tester 2008).

SALINE STRESS AND PLANT RESPONSES

Compatible solutes

Plants accumulate many metabolites (compatible solutes) in the cytoplasm to increase their hyperosmotic tolerance against salt stress-induced water loss from the cells. This process is also required to balance the osmotic potential of Na^+ and Cl^- being sequestered into the vacuole (Wyn Jones *et al.* 1977). Various compounds such as sugars (chiefly fructose, sucrose and glucose), sugar alcohols (mannitol, glycerol and methylated inositols), complex sugars (trehalose, raffinose and fructans), quaternary amino acid derivatives (proline (Pro), glycinebetaine (GB), β-alaninebetaine, prolinebetaine), tertiary amines (1,4,5,6-tetrahydro-2-methyl-4-carboxyl pyrimidine) and sulfonium compounds (choline-*O*-sulfate), dimethylsulfoniopropionate (DMSP) have been suggested to accomplish this function (Flowers and Colmer 2008). The high concentration of compatible solutes exists primarily in the cytosol, to balance the high concentration of salt outside the cell on one side, and on the other, to counteract the high concentrations of sodium and chloride ions in the vacuole (Kavikishore et al. 2005). The physicochemical basis of the protective effect of osmolytes involves the exclusion of osmoprotectant molecules from the hydration sphere of proteins (Timasheff 1992), which creates a situation where native protein structures are thermodynamically favored because they present the least possible surface area to the water (Rontein *et al.* 2002)

Pro level increases up to 100 times under saline condition in comparison to non- saline in a large variety of plants and makes up to 80% of the total amino acid pool. The accumulation and protective role of Pro has been observed in both prokaryotic and eukaryotic organisms, which is considered as either to be symptomatic of salt induced stress or to have a protective role other than osmotic regulator (Chen and Dickman 2005). Pro-accumulation and enhanced synthesis of Pro under dehydrated conditions (drought or salinity) have been involved in alleviation of cytoplasmic acidosis and sustaining $NADP^+/NADPH$ ratios at required levels for metabolism (Hare and Cress 1997), and thus supporting redox cycling (Babiychuk *et al.* 1995). We have also reported that salt stress remarkably enhanced Pro accumulation, which implies the involvement of Pro accumulation to contribute osmotic adjustment during salinity. Pro stabilizes proteins, membranes and subcellular structures and protects cellular functions by scavenging reactive oxygen species (Gautam and Singh 2009).

GB, a quaternary ammonium compound, has been shown to accumulate in response to salt stress and plays an important role in a range of families of flowering plants, bacteria, cyanobacteria, algae and fungi (Storey *et al.* 1977). GB is synthesized from choline in two steps, the first being catalyzed by choline monooxygenase leading to synthesis of betaine-aldehyde, which is further oxidized by betaine-aldehyde dehydrogenase (Russell *et al.* 1998). GB has been shown to protect higher plants against salt/osmotic stresses by playing an osmolyte role (Jagendorf and Takabe 2001). The correlation between protective effect of GB and antioxidative defense system has also been observed in chilling-stressed tomato (Park *et al.* 2006), drought- or salt-stressed wheat (Ma *et al.* 2006; Raza *et al.* 2007) and salt-stressed suspension cultured tobacco BY2 cells (Hoque *et al.* 2007).

Sugars are readily accessible and energetically inexpensive sources of osmotica and accepted as an osmolyte (Hasegawa *et al.* 2000). The disadvantage in accumulating sugars is that they are the energy supply of the cells and accumulation in inert or inaccessible form reduces their availability. Sugars such as glucose, fructose, sucrose fructans and starch provide osmoprotection, osmotic adjustment carbon storage and radical scavenging (Parida *et al.* 2002; Zhu 2002) under stress condition. The accumulation of polyols either straight chain metabolite such as mannitol and sorbitol or cyclic compounds such as myoinositol and its derivative onoitol and pinnitol is directly correlated with salinity and drought tolerance in many lower and higher plants (Bohnert *et al.* 1995; Parida and Das 2005). *Myo*-inositol serves as facilitator of sodium uptake to the vacuole or apoplast and long distance transport. It might also protect cellular structures by scavenging active O_2 through their interaction with membranes, protein complexes or enzymes. The cyclic sugar alcohols, pinnitol and ononitol are stored in a variety of species, which are consistently exposed to saline conditions or accumulate in tolerant species when exposed to saline environments. The proposed synthetic pathway consists of methylation of *myo*-inositol to the intermediate ononitol followed by epimerization to pinnitol. Sorbitol, a sugar alcohol of glucose is found in a variety of plant species, usually as a constituent of seeds. Sorbitol accumulation has been reported in seeds of many crop plants (Kuo *et al.* 1990). In Rosaceae species, it functions as a translocated carbohydrate and is also reported in vegetative parts in the halo-tolerant *Plantago maritima* (Ahmad *et al.* 1979). Increasing salinity from 0 to 400 mol m^{-3} resulted in an eightfold increase of sorbitol concentration in shoot tissues and a 100-fold increase in root tissues. Its accumulation serves an osmo-regulatory function and may contribute to the desiccation tolerance of the mature embryo. The conversion of glucose to its sugar alcohol is catalysed by aldose reductase. An aldose reductase-like protein accumulates during the period of embryo maturation in barley when desiccation tolerance is obtained (Bartels *et al.* 1991).

Antioxidative system

Exposure of plants to unfavourable environmental conditions can increase the production of reactive oxygen species. During salinity-induced oxidative stress, two primary processes are involved in the formation of ROS during photosynthesis. One is the direct photoreduction of O_2 to the superoxide radicle by reduced electron transport components associated with PS I (Mehler reaction), and other are the reactions linked to the photorespiratory cycle, including Rubisco in the chloroplast and glycolate-oxidase and CAT-peroxidase reactions in the peroxisome. These processes initiate chain reactions that produce more harmful oxygen radicals (Hsu and Kao 2003). These cytotoxic reactive oxygen species (ROS) can destroy normal metabolism through oxidative damage of lipids, proteins, and nucleic acids when they are produced in excess (McCord 2000). Plants have evolved efficient systems for ROS removal, which include specific ROS-scavenging enzymes like superoxide dismutase (SOD; EC 1.15.1.1), ascorbate peroxidase (APX; EC 1.11.1.11), catalase (CAT; E.C 1.11.1.6), glutathione reductase (GR; EC 1.6.4.2) and glutathione peroxidase (GPX; EC 1.11.1.9). and small non-enzymatic molecules that act as ROS scavenger such as ascorbate, glutathione, tocopherol, flavonoids, anthocyanines, polyphenolic compounds and carotenoids.

ROS are regularly synthesized in the chloroplast (Asada 1992) and mitochondria (Rich and Bonner 1978), though some quantity is also reported to be produced in microbodies (Lindquist *et al.* 1991). SOD is a metalloenzyme that catalyze the disproportionation of toxic superoxide radicles to hydrogen peroxide (H_2O_2) and O_2 and thus play a very crucial role in the maintenance of low concentration of toxic radical. SOD_s occurs in three different molecular forms which contain copper and zinc (CuZn) iron (Fe) or manganese (Mn) as prosthetic metals. CuZn-SOD_s are the major enzymes in plants and are known to be localized in chloroplast (Asada 1992), cytosol (Bowler *et al.* 1994) and peroxisomes of oil seeds (Corpas *et al.* 1998). Mn SOD_s occur mainly in mitochondria and are also found in peroxisomes and in chloroplasts while FeSOD_s have frequently been shown to be present in prokaryotes but only rarely in the chloroplasts of higher plants. Peroxidases (EC. 1.11.1.7) function as effective quenches of reactive intermediary forms of oxygen and peroxy radicals produced under stress (Zhang and Kirkham 1994). Peroxidases form large families with substrate specificity, its function are ubiquitous in plants, and catalyze the oxidation of cellular components by either H_2O_2 or hydroperoxides. Ascorbate Peroxidase that uses ascorbate as its reducing substrate and is the major H_2O_2 scavenging enzyme in plants under normal and stress conditions and occur as several isozymes localized in different cellular compartments like cytosol microbodies, chloroplasts, etc. (Madhusudhan *et al.* 2003). Enzyme which requires guaiacol (2-methoxyphenol) is known as guaiacol peroxidase (GP_{ox} EC 1.11.1.7). There is a significant reactivity differences between ascorbate specific and guaiacol specific Peroxidase. They also differ in their physiological roles. Reaction catalyzed by AP_{ox} prevents accumulation of excess H_2O_2 and this provides for cell defense against oxidative stress (Yoshimura *et al.* 2000). In contrast guaiacol peroxidases also exist in several isoenzymic forms and are located in cytosol, vacuole, cell wall, extra cellular space, oxidize a wide range of organic substrates and are involved in processes like lignification of cell wall as well as in wound healing (Gazaryan *et al.* 1996).

The role of GR in H_2O_2 scavenging in plant cells has been well established in Halliwell-Asada enzyme pathway (Bowler *et al.* 1992). Elevated levels of GR activity perhaps increase the ratio of $NADP^+/NADPH$ thereby ensuring availability to $NADP^+$ to accept electron from photosynthetic electron transport chain, minimizing the formation of GSH/GSSG helps in regeneration of ascorbate which is necessary for the activation of several chloroplastic CO_2 fixing enzymes and accumulation of GSH that ultimately confers tolerance to stress in plants (Baisak *et al.* 1994).

The harmonized activities of the multiple forms of these enzymes in different subcellular compartments achieve a balance between the rate of formation and removal of ROS, and sustain H_2O_2 at the required levels for cell signaling. It is now widely accepted that the degree of oxidative cellular damage in plants exposed to abiotic stresses is controlled by the capacity of the antioxidative systems (Acar *et al.* 2001; Türkan *et al.* 2005). A correlation between antioxidant capacity and salinity tolerance has been reported in several plant species such as rice (*Oryza sativa* L.)(Demiral and Türkan 2004, 2005), wheat (*Triticum aestivum* L.) (Meneguzzo *et al.* 1999), pea (*Pisum sativum* L.)(Hernández *et al.* 1995, 2000), sesame (*Dalbergia sissoo* L.)(Koca *et al.* 2007), Indian mustard (*Brassica juncea* L.) (Yusuf *et al.* 2008), corn (*Zea mays* L.) (Szalai and Janda 2009). Furthermore, transgenic plants overexpressing ROS-scavenging enzymes, such as SOD (Breusegem *et al.* 1999; Alscher *et al.* 2002), APX (Wang *et al.* 1999), GR (Foyer *et al.* 1995) and GPX (Roxas *et al.* 1997, 2000) showed enhanced tolerance to osmotic, temperature, photoinhibition and oxidative stresses. Transgenic tobacco plants overexpressing APX in their chloroplasts showed enhanced tolerance to salt, PEG and water stresses (Badawi *et al.* 2004) and those expressing glutathione-*S*-transferase constitutively showed protection against both cold and salt stresses (Roxas *et al.* 1997). Mohamed *et al.* (2003) has recently shown that tomato plants that are expressing bacterial catalase gene in their chloroplasts were protected against the photo-oxidative stress caused by paraquat treatment, drought stress and chilling stress.

Salt stress-induced proteins

Plants frequently produce new proteins in response to abiotic stress, which is considered to be a signaling and defense response. Proteins induced by stress are categorized as those induced by stress and ABA, induced by stress but not by ABA and inducible by ABA only. LEA (late embryogenesis abundance) proteins, which are ABA-inducible group of proteins and originally suggested to be associated with desiccation tolerance during seed maturation, are also induced by salinity, drought and cold temperature (Close 1997). LEA proteins have been placed in different groups on the basis of amino acid sequence homology. The *lea* genes encode proteins that are overwhelmingly hydrophilic, remain stable at high temperature and are basic. Most of these proteins lack cysteine and tryptophan, are not compartmentalized or transported within the cell, and are likely to be located in the cytosol. These proteins protect the cellular structure and components, e.g. membranes and proteins/enzymes from the effects of water loss during salt-stress.

The LEA proteins are divided into six groups: Group 1-D19-LEA, Group 2-D11-LEA also called dehydrins, Group 3-D7-LEA, Group 4-D113-LEA, Group 5-D95-LEA, and Group 6 –D29-LEA may be similar to group 3.

Osmotin (m.wt.26 KDa), a polypeptide, is induced by salinity stress (Bressan *et al.* 1987), occurs in two forms Osmotin I (water soluble) and Osmotin II (detergent soluble) in the ratio of 2:3 forms (Singh *et al.* 1987b): Osmotin II appears more resistant to proteolysis than osmotin I. Several HSPs (Heat shock proteins) are also expressed in response to salt stress (Borkird *et al.* 1991). These act as chaperones to prevent denaturation and to help denatured protein regain their native formation. These are mostly encoded by nuclear genes but are localized in different cell compartments. Based on their mode of expression hsp genes fall into two categories (i) those that are constitutively expressed often referred to as heat shock cognates (hsc), (ii) those that are strongly induced under heat stress (hsp) (Vierling 1991; Singla *et al.* 1997). Adequate and continued water supply in plants subjected to salt stress is an important aspect of plant salt tolerance. Chrispeels *et al.* (1999) reported certain proteins (water channels termed as aquaporins) might be involved in transport of water and mineral nutrients across the membranes of plant cells under salt stress. Regulation of activity of these aquaporins may be due to changes in oligomerization, by phosphorylation or possibly by cycling through the endomembrane system as reported in animal system (Yang and Verkman 1997).

SALICYLIC ACID-INDUCED CHANGES IN PLANTS

The evidence concerning improvement of salt tolerance by SA depends on metabolic conditions of the plants. Application of exogenous SA counteracted salt stress-induced growth inhibition in a salt-tolerant wheat genotype, but no improvement occurred in a salt-sensitive cultivar (Arfan *et al.* 2007). Studies suggest that SA-induced fine-tuning of the net ion uptake by the root, vacuolar compartmentalizetion of Na^+ and facilitate osmotic adjustment through somehow signal transduction mechanism in a saline environment.

Signal perception/signal transduction during salinity stress

Numerous signal or signal-like molecules have now been identified and presumed, through some evidence, to function in plants as mediators of osmotic adaptation (Tuteja and Sopory 2008). A signal or any environmental stimuli must be sensed by receptor/receptors present in the plasma membrane, cytosol or other cellular components. There are multiple pathways of signal transduction systems operating at cellular level for expression of gene regulation. Initial events of salinity, may effect osmoticum and bring changes in the function of plasma membrane. Na^+ is passively transported into the cytosol by non-selective cation channels (NSCCs), which is immediately perceived towards exclusion through two operational mechanisms. First, efflux of cytosolic Na^+ across the plasma membrane SOS1- Na^+-H exchanger located on plasma membrane. Second, compartmentalization of Na^+ into vacuole by Na^+-H antiporter, NHX1. (Both the transporter activities require an H^+ gradient generated by plasma membrane H^+-ATPase or by a vacuolar H^+-ATPase) and by vacuolar H^+pyrophosphatase (AVP1) (**Fig. 1**)

Accumulation of osmoprotectants and heat shock proteins, some of which are mediated through phytohormones ABA, JA and SA (Overmyer *et al.* 2003). SA has appeared as a new phytohormone biosynthesized from the phenylalanine in plant metabolism and considered as an important signaling molecule modulating plant responses to biotic and abiotic stresses.

Components of the salt/drought stress signal-transduction pathway are difficult to identify, ABA has appeared as one such component operating signal transducing element for desired gene product (Zhu 2002). Both ABA-dependent and -independent pathways are identified for the induction of stress-related genes (Xiong *et al.* 2002). ABA dependent salt or osmotic response genes are under complex regulation. An osmotic stress activated SA-induced protein kinase (MAPK family) was observed in tobacco cells which up regulated the activity of Abscisic aldehyde oxidase in *Solanum lycopersicum* L. during ABA biosynthesis (Mikolajczyk *et al.* 2000; Szepesi *et al.* 2009).

Role of salicylic acid in salinity stress management

Investigations show the role of SA in modulating plant responses to a wide range of osmotic/ and or oxidative stresses. The maintenance of growth and development in saline environments is associated with osmotic adjustment, and with the synthesis of osmoprotectants/ compatible osmolytes or in some halophytes, with the sequestration and accumulation of Na^+ in the vacuole (Ramani *et al.* 2006). Concentration based regulation of acclimation to salt-stresses by exogenous application of SA in plants may become a specific tool to understand the physiology, molecular biology and biotechnology of plants. Plants respond to stress by the synthesis of signaling molecules. These activate a range of signal transduction pathways. Several such signaling molecules have been identified in plants as calcium, jasmonic acid, ethylene and SA. The role of SA as a defense signal has been well established in plants (Klessig and Malamy 1994). SA has qualified as a plant hormone due to its phy-

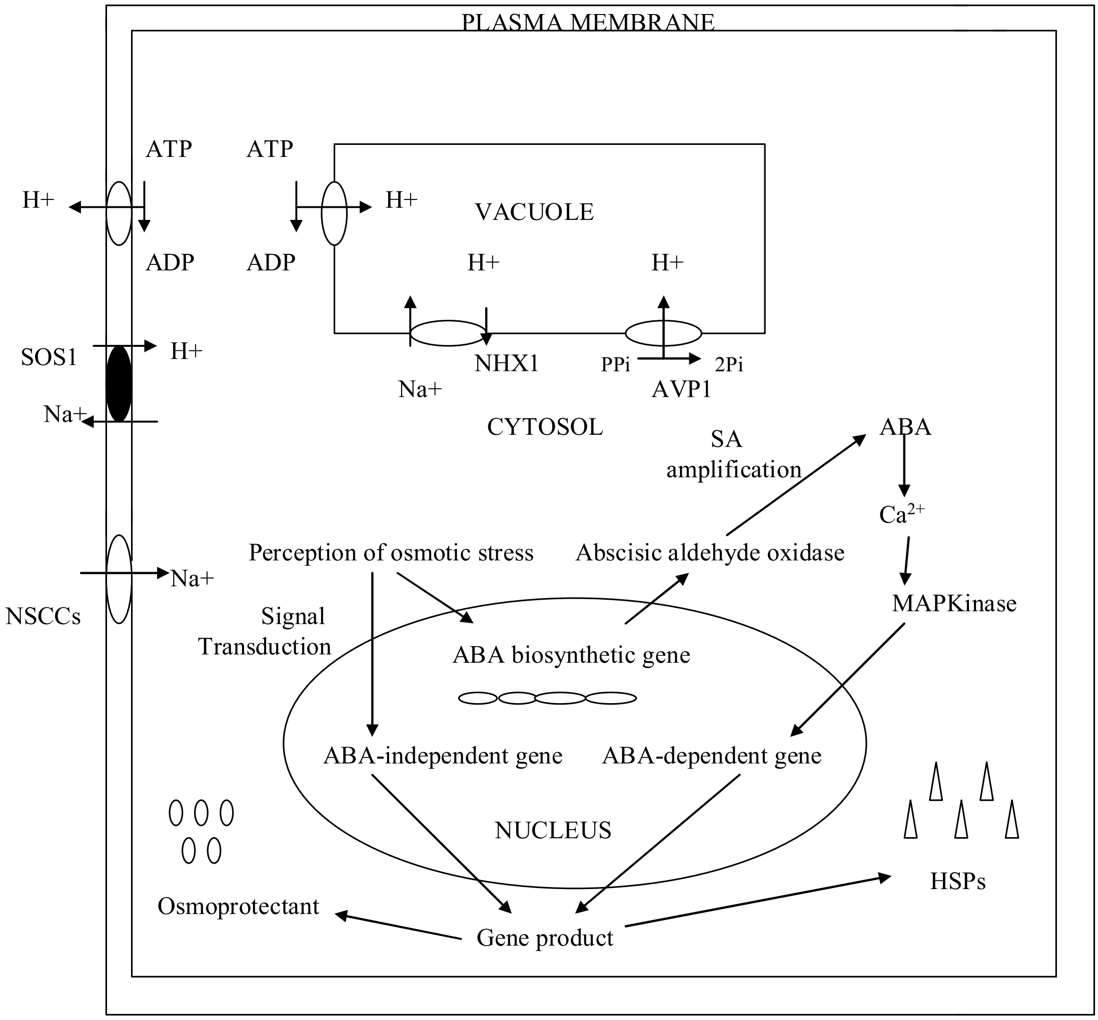

Fig. 1 Ion homeostasis and probable signal transduction pathways of salt tolerance. Na^+ is passively transported into the cytosol by non-selective cation channels (NSCCs). For cellular homeostasis, two mechanisms operate; one is exclusion of Na^+ across the membrane (SOS1, a Na^+-H^+ exchanger located at plasma membrane). Second is the compartmentalization of Na^+ into vacuoles (NHX1), where Na^+ is less toxic. Salinity induced osmotic stress is perceived through both ABA-dependent and ABA-independent signaling. Na^+ stressed gene expression of ABA biosynthesis is stimulated through SA amplification of AAO protein (Szepesi *et al.* 2009). ABA induced gene expression involve Ca^{2+} coupled signal transduction cascade(s), may regulate genes for required osmolytes and HSPs biosynthesis (Leung and Giraudat 1998).

siological and biological roles in plants (Raskin 1992). SA has been suggested as signal transducer or messenger under stress conditions (Klessig and Malamy 1994).

Numerous studies have indicated that exogenous application of salicylic acid to the stressed plants can potentially alleviate the toxic effects, generated by salinity. An enhanced tolerance against salinity stress was observed in tomato plants raised from the seeds soaked in salicylic acid and was presumed to be due to the enhanced activation of some enzymes viz. aldose reductase and ascorbate peroxidase and to the accumulation of certain osmolytes such as proline (Tari *et al.* 2002, 2004; Szepesi *et al.* 2005). Accumulation of large amounts of osmolytes (proline) is an adaptive response in plants exposed to stressful environments (Rai 2002). Wheat seedlings accumulated large amounts of Pro under salinity stress, which was further, increased when salicylic acid was applied exogenously, thereby alleviating the deleterious effects of salinity (Shakirova *et al.* 2003). The exogenous application of salicylic acid prevented the lowering of IAA and cytokinin levels in salinity stressed wheat plants resulting in the betterment of cell division in root apical meristem, thereby increasing growth and productivity of plants (Shakirova *et al.* 2003). These authors also reported that the pre-treatment with SA resulted in the accumulation of ABA, which might have contributed to the pre-adaptation of seedlings to salinity stress as ABA induces the synthesis of a wide range of anti-stress proteins, thereby providing protection to the plants. Further, the treatment also lowered the level of active oxygen species and therefore the activities of SOD and POX were also lowered in the roots of young wheat seedlings (Shakirova *et al.* 2003). These findings indicate that the activities of these antioxidant enzymes are directly or indirectly regulated by salicylic acid, thereby providing protection against salinity stress (Sakhabutdinova *et al.* 2004). The possible existence of positive amplification loops involving NADPH oxidases in ROS signaling has been suggested in several studies (Dat *et al.* 2003; Rizhsky *et al.* 2004). These loops might be activated by low levels of ROS and result in enhanced production and amplification of the ROS signals in specific cellular locations. The accumulation of ROS in cells might activate the ROS scavenging pathways and result in the suppression of ROS in specific cellular locations or the entire cell. Overmyer *et al.* (2003) proposed that SA might be involved in this positive amplification loop and amplifies signals leading to defense responses. Exogenous application of salicylic acid enhanced the photosynthetic rate and also maintained the stability of membranes, thereby improved the growth of salinity stressed barley plants (El Tayeb 2005). The damaging effects of salinity were also alleviated by exogenous application of SA in Arabidopsis seedlings (Borsani *et al.* 2001). Kaydan *et al.* (2007) observed that pre-sowing soaking treatment of seeds with SA positively affected the osmotic potential, shoot and root dry mass, K^+/Na^+ ratio and contents of photosynthetic pigments (chlorophyll *a*, *b* and carotenoids) in wheat seedlings, under both saline and non-saline conditions. The loss of growth, photosynthetic parameters and the activities of enzymes (nitrate reductase and carbonic anhydrase) as a result of salinity stress in *B. juncea* was revived when salicylic acid was sprayed to the foliage, at 30 days stage. Further the activities of various antioxidant enzymes (CAT, POX and SOD) were increased with a concomitant increase in proline content as a result of salinity exposure and/or SA treatment, thereby providing enhanced tolerance against salinity stress (Yusuf *et al.* 2008).

CONCLUSION AND FUTURE PROSPECTS

Secondary metabolism and transgenic plants has become a standard tool in plant stress biology. These technologies have mainly been utilized to model systems and have greatly enlarged the knowledge of mechanisms of tolerance. Phytohormones basically salicylic acid improves acclimation to salt stress by ion exclusion and/or compartmentalizetion, osmotic adjustments, reduction in lipid peroxidation, stress induced synthesis of protein kinases (SIPK), regulation of oxidative system and also enhanced antioxidant activity to combat the lethal oxidative events. Recently, it has been observed that reversible protein phosphorylation is likely to play a crucial role in mediating intracellular response to external stimuli in plants and suggest that this family of kinases may be involved in stress-signal transduction pathways in plants.

The molecular analysis of stress responses has arrived at a stage where research can facilitate a large collection of characterized genes. Identification and characterization of genetic loci for abiotic stress resistance could be an effective analytical tool. The use of novel approaches combining genetic, biochemical and molecular techniques should provide results in near future for food security.

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