INTRODUCTION

Soil salinity is a major abiotic stress that adversely affects crop productivity. High salinity conditions have been found on earth from early civilizations and have been causing substantial yield reductions in agriculture throughout the world. The problem of soil salinity is increasing due to number of factors such as, irrigation, improper drainage, seawater in coastal areas, and salt accumulation in arid and semi-arid regions. Salinity is detrimental to plants as it causes nutritional constraints by decreasing the uptake of mineral nutrients, primarily nitrogen, phosphorus, potassium and calcium, ion toxicity and osmotic stress. Under salinity, Na⁺ and Cl⁻ ions penetrate the hydration shells of proteins and interfere with the function of these proteins (Smirnoff 1998). The toxicity of ions, osmotic stress and nutritional imbalances under salinity cumulatively lead to oxidative stress in plants (Serrano et al. 1999; Zhu 2001).

It has been reported that about one-third of world-irrigated land is affected by soil salinity (El Saied 1997). The United Nations Environment Program estimates that 20% of the agricultural land and 50% of the crop land in world is salt-stressed (Flowers and Yeo 1995; Baltrėnas and Kazlauskiénė 2007).

Around the world, 100 million ha or 5% of the arable land is adversely affected by high salt concentrations (Ghassemi et al. 1995). In India about 7-12 million ha of land are known to have been degraded by salinity with varying degrees of salt accumulations (NBSS and LUP 2005). The problem of salinity is more acute in the semi-arid and arid tracts of Indo-Gangetic alluvial plains where about 40% of the total affected area is concentrated (Agarwal et al. 1979). Besides, an additional area of about 15-20 million ha of land in canal irrigated tracts runs the risk of being degraded through the influence of salts (Abrol 1986). In dry areas, salt concentration increases in the upper soil layer due to high evaporatory water loss that exceeds precipitation (Ebert et al. 2002).

Based on the capacity of plants to grow under high salt conditions, they are classified as halophytes or glycophytes. A halophyte is a plant that naturally grows, where it is affected by salinity in the root area or by salt spray, such as in saline semi-deserts, mangrove swamps, marshes and sloughs, and seashores. An example of a halophyte is the salt marsh grass Spartina alterniflora (smooth cordgrass). Relatively few plant species are halophytes, perhaps only 2% of all plant species. A large majority of plant species is glycophytes, and are damaged fairly easily by salinity (Glenn et al. 1999). Halophytes, plants that survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more, constitute about 1% of the world's flora (Flowers and Colmer 2008), while glycophytes can not grow in the presence of high salt concentrations.

Plant salt tolerance is necessary for sustainable food production on marginal lands and to potentially improve overall crop yield. Plant salt tolerance mechanisms can be
grouped into cellular homeostasis (including ion homeostasis and osmotic adjustment) or stress damage control (repair and detoxification and growth regulation) (Hirt and Shinzaki 2004). As halophytes can tolerate high salt concentrations the inherent mechanism and processes may be used as a tool for incorporating tolerance in other plants. In addition to halophytes, other plant types also have biochemical and physiological strategies for salt tolerance. These mechanisms can be studied and enhanced in the plant types that are not tolerant to salt stress. These mechanisms are: (i) control of ion uptake and accumulation in leaves, (ii) synthesis of compatible osmolytes, (iii) alteration in photosynthetic pathway, (iv) induction of antioxidative enzymes and (v) induction of phytohormones (Parida and Das 2005).

Under salt stress, plants adapt several mechanisms to protect themselves. A wide range of second messengers have been implicated to a variety of stresses. Several techniques for either alleviating the salt effects or inducing salt tolerance by manipulating soil amendments, plant breeding, methods of sowing, and management practices have been tried but not much success has been achieved so far and the problem continues to be a serious limiting crop yields. Salinity is known to disturb the endogenous hormonal balance in plants. In general, the levels of growth promoters are reported to decrease and of inhibitors to increase in saline conditions (Levitt 1980). Plant regulators are known to control internal metabolism therefore, attempts need be made to explore the possibility of using these for alleviating salt stress-induced physiological effects. Plant growth regulators are effective in reducing the adverse effects of salinity. Since long presoaking of seeds with optimal concentration of phytohormones has been shown to be beneficial to growth and yield of some crop species grown under saline conditions by increasing nutrient reserves through increased physiological activities and root proliferation (Singh and Dara 1971; Parida and Das 2005). Concerted attempts have been made to mitigate the harmful effects of salinity by application of plant growth regulators (Datta et al. 1998). Thus, the detrimental effects of high salts on the early growth of wheat (Triticum aestivum) seedlings may be reduced to some extent by treating seeds with the proper concentration of a suitable hormone (Darra et al. 1973). Studies have previously been demonstrated that salicylic acid (SA) induces tolerance to salinity stress with altered water relations and consequent changes in solute concentration (Senaratna et al. 2000, 2003). Senaratna et al. (2007) have reported SA-induced salinity tolerance in a variety of genetically diverse plant taxa explaining different mechanisms of salinity tolerance.

**SA Salicylic Acid**

SA was first discovered as a major component in the extracts from *Salix* (willow), whose bark from ancient time was used as an anti-inflammatory drug (Andrews 1997). SA is in fact a phenol, ubiquitous in plants generating a significant impact on plant growth and development, photosynthesis, and survival of plants. SA has been known to be present in some plant tissues for quite some time, but has only recently been recognized as a potential plant growth regulator (PGR). The role of SA in the defense mechanisms against biotic and abiotic stresses has been well documented (Yalpani et al. 1999; Szalai et al. 2005). SA has been found to promote flowering, stimulates plant pathogenesis protein production, enhances longevity of flowers, inhibits ethylene biosynthesis, and reverse the effects of ABA. Relatively little work has been done on the influence of SA on plant metabolism. Salicylic acid plays in important role in flower induction, growth and development, ethylene biosynthesis, stomatal behaviour and respiration (Raskin 1992). It is important in disease resistance (Larkindale and Huang 2004) and to control the activities of antioxidant enzymes and decreasing the contents of Na⁺ and Cl⁻ in leaves, the decreases in plant dry mass, net photosynthetic rate and seed yield due to 50mM NaCl were reduced with the application of 0.5 mM SA given to NaCl treated plants. The decreases in these charac-

**Biosynthesis**

The biosynthesis of SA in plants occurs via the shikimate-phenylpropanoid pathway (Zenk and Müller 1964), where phenyl alanine is first converted to trans-cinnamic acid (t-CA) by phenylalanine ammonia lyase (PAL). This enzyme is induced by a range of biotic and abiotic stresses and is a key regulator of the phenylpropanoid pathway, which yields a variety of phenolics with structural and defense related functions (Yalpani et al. 1993). Two pathways for the formation of SA have been reported in plants. Trans-cinnamic acid is either hydroxylated to o-coumaric acid before oxidation of the side chain, or the t-CA side chain is shortened to benzoic acid (BA), which is in turn hydroxylated to SA (Sticher et al. 1997). The conversion of phenylalanine to cin-

**Physiological effects of Salicylic Acid on Plants**

SA has been known to be present in some plant tissues for quite some time, but has only recently been recognized as a potential plant growth regulator (PGR). The role of SA in the defense mechanisms against biotic and abiotic stresses has been well documented (Yalpani et al. 1999; Szalai et al. 2005). SA has been found to promote flowering, stimulates plant pathogenesis protein production, enhances longevity of flowers, inhibits ethylene biosynthesis, and reverse the effects of ABA. Relatively little work has been done on the influence of SA on plant metabolism. Salicylic acid plays in important role in flower induction, growth and development, ethylene biosynthesis, stomatal behaviour and respiration (Raskin 1992). It is important in disease resistance (Larkindale and Huang 2004) and to control the activities of antioxidant enzymes and decreasing the contents of Na⁺ and Cl⁻ in leaves, the decreases in plant dry mass, net photosynthetic rate and seed yield due to 50mM NaCl were reduced with the application of 0.5 mM SA given to NaCl treated plants. The decreases in these charac-
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Characteristics were limited to 6.90, 1.53 and 0.56% in Pusa Vishal and 26.80, 15.38 and 20.47% in Tram due to the treatment 0.5 mM SA plus 50 mM NaCl compared to control (Syeed 2008).

Moharekar et al. (2003) reported that the total Chl (a and b) content decreased significantly in wheat with an increase with the SA concentration. However, in mungbean, Chl content was lower in control plants than in SA treated ones but decreased significantly with the increase in SA concentration (Syeed 2008). A reduction in Chl content in barley (Hordeum vulgare) and mungbean leaves following the application of SA was previously found by Pancheva et al. (1996) and Anandhi and Ramanujam (1997).

Moharekar et al. (2003) reported that Chl a/b ratio decreased significantly with an increase in SA concentration in wheat. However, in mungbean it remained constant. In contrast to Chl, the content of total carotenoids (Car) increased significantly with an increase in SA concentration in both the crops (Syeed 2008). In Arabidopsis thaliana leaves, 1 mM SA application caused an increase in Car content, whereas 5 mM SA caused a decrease in the Car content in comparison with the control (Rao et al. 1997). Moharekar et al. (2003) reported that an increase in SA concentration stimulated Car accumulation in wheat and mungbean plants. They also reported that the size of xanthophyll pool increased significantly with the increase in SA concentration. Under stress, zeaxanthin and possibly antheraxanthin have been found responsible for the quench-
ching of excess excitation energy (Gilmore and Yamamoto 1993). The size of xanthophylls has been found increased in plants grown under stress conditions (Demming-Adams et al. 1989, 1995; Logan et al. 1996).

SA is in fact, the most important systemic signal molecule. Exogenous application of SA has induced resistance in some plants (Conrath et al. 1995; Lawton et al. 1996; Amareddi-Chandra et al. 2001; Guleria et al. 2001; Negi and Prasad 1997, 2001). The effect of SA on the physiological processes of the plants is variable, promoting some processes and inhibiting others (Raskin 1992). Significant reductions in transpiration and stomatal aperture were obtained, but SA has also been reported to reverse the stomatal closure induced by ABA (Rai et al. 1986). Exogenous applications of SA to different species of crops have been shown to elicit effects on yield and yield components. An increase in the number of pods and yield has been found in mungbean (Singh and Kaur 1980) and common bean (Phaseolus vulgaris) (Rendon 1983; Lang 1986). Other effects of SA and its regulatory role in plant physiology included inhibiting ethylene biosynthesis, interfering with membrane depolarization, blocking wound responses, and an increase in net photosynthetic rate and chlorophyll content in soybeans (Glass and Dunlop 1974; Leslie and Romani 1988; Zhao et al. 1995). It has also been recognized that SA is required in the signal transduction chain for inducing systemic acquired resistance (Metraux et al. 1990; Gaffney et al. 1993; Vernooij et al. 1994). Zhao et al. (1995) reported an increase in net photosynthetic rate that they ascribed to an enhancement of leaf enzyme activity by SA. Gutiérrez-Coronado et al. (1998) reported that, in soybean, shoot growth was increased with the concentrations of SA. The concentrations of SA significantly increased root length. Singh (1993) found that SA stimulated root formation in young shoots of ornamental plants and Li and Li (1995) reported the formation of adventitious roots on hypocotyl cuttings of mungbean.

Exogenous application of SA enhanced the drought and salt stress resistance of plants (Senaratna et al. 2000; Tari et al. 2002), but the results were contradictory and depended on the developmental phase of plants (Borsani et al. 2001) or on the experimental conditions (Neemeth et al. 2002).

Szepesi et al. (2005) reported that the $10^{-7}$ M SA pre-treatment in tomato decreased the osmotic stress-induced reduction in relative water content, but this alleviating effect was not so pronounced at $10^{-6}$ M SA concentration. A small increase was observed in the water and osmotic potential of SA pretreated samples, but in case of the pressure potential the changes were higher. Under the influence of salt stress the osmotic potential decreased more at the SA pretreatments moderated it at both $10^{-7}$ M and $10^{-6}$ M concentrations. SA pretreatments reduced $K$ contents of leaves under salt and non-ionic osmotic stress. Compared to the NaCl-treated plants, SA decreased the Na/K ratio in the roots and increased it significantly in the leaves. SA improved the photosynthetic performance of plants under stress conditions (Ananieva et al. 2002), and $Chl$ $a$ fluorescence gave insight into the ability of plant to tolerate environmental stresses. Szepesi et al. (2005) reported that at low photosynthetic light intensity (165 $\mu$mol m$^{-2}$ s$^{-1}$) the effective quantum yield was only slightly affected in NaCl-treated tomato samples, but it was significantly reduced under non-ionic osmotic stress. This was partially overcome if the plants were pretreated with SA. SA pretreatment might improve the gross rate of carbon assimilation during osmotic stress.

Pan et al. (2006) reported that SA application reduced leaf injury in pea (Pisum sativum) caused by heat stress and induced the synthesis of heat shock proteins (Hsp70 and Hsp17.6). Further, membrane lipid peroxidation caused by the heat stress was found to decrease, suggesting that plant’s thermo-tolerance developed as a result of SA application. A rapid transient increase of endogenous free SA and a subsequent enrichment in Hsp70 were both elevated by heat acclimation. Gunes et al. (2007) reported that exo-
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genously applied SA increased plant growth of maize significantly both in saline and non-saline conditions. As a consequence of salinity stress, lipid peroxidation, measured in terms of malondialdehyde content and membrane permeability decreased by SA. UV-absorbing substances and H$_2$O$_2$ concentration were increased by increasing levels of SA. SA also strongly inhibited Na$^+$ and Cl$^-$ accumulation (also observed in authors laboratory in mungbean, the effects of SA were reversed with water in control). The application of 0.5 mM SA on plants fed with 50 mM NaCl decreased the concentrations of sodium and chloride in comparison to the control. The decreases in sodium and chloride concentrations were 30.93 and 27.42% in Pusa vishal and 23.42 and 19.23% in Tram (unpublished data), but stimulated nutrients accumulation. It was concluded that SA could be used as a potential growth regulator to improve plant salinity stress resistance. Increase in growth parameters of salt-stressed plants in response to SA may be related to the induction of growth characteristic and protective role of SA on membranes that increase the tolerance of plants to damage (Wang et al. 2007). Exogenously applied SA caused increase in stomatal conductance, but it did not change the substomatal CO$_2$ suggesting that SA applied as a foliar spray reversed the salt-induced stomatal closure (Noreen and Ashraf 2008). However, it was shown that SA may have affected certain metabolic factors in carbon uptake or fixation of Rubisco enzyme, and/or photosynthetic carbon reduction cycle (Arfan et al. 2007). Stimulation of growth after supplementation of SA has been reported in maize plants (Gunes et al. 2007). It is also considered as a plant growth regulator (Misra and Sexana 2009), which plays an important role in regulating a number of plant physiological processes including photosynthesis (Arfan et al. 2007). It was found that SA-induced increase in growth could be related to SA-induced considerable enhancement in net photosynthetic rate. In our study, the application of higher concentration of SA (1.0 mM) proved inhibitory on the characteristics under saline condition. On the similar lines, Kovack et al. (2009) showed that low concentration of SA (50 μM) exhibited growth promoting and high concentration of SA (250 μM) exhibited growth inhibiting properties in Matricaria chamomilla plants.

Several studies published indicate the role of SA as cell stress protectant through induction of antioxidative system. SA has been reported to influence the activities of antioxidative enzymes differentially. In general, authors found enhancement in the activities of antioxidative enzymes such as superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX) and glutathione-S-transferase (GST) following SA application. Application of 0.5 mM SA on mungbean plants treated with 50 mM NaCl exhibited higher increase in the activities of antioxidative enzymes compared with the increase observed in 50 mM NaCl treatment. The increase in SOD, GR and APX activities of Pusa Vishal and Tram was 40.42, 41.74 and 46.88% and 39.56, 28.64 and 38.54%, respectively due to 50 mM NaCl plus 0.5mM SA in comparison to 50 mM NaCl in control. Stimulation of tomato seeds with SA resulted in the synthesis of enzymes as well as by some kind of direct modulation of the enzyme molecules (Singh and Srivastava 1987). Kauss et al. (1992) also observed increase in peroxidase activity in parsley (Petroselinum crispum) cells in response to 2,4-dichloro-isonicotinic acid and SA spray. The increase in peroxidase activity after SA spray has also been reported in salt-exposed rice seedlings (Cai and Zheng 1997). Shim et al. (2003) reported a significant and dose-dependent increase in CAT activity of rice seedlings. They negatively correlated this increase in SA content with CAT activity and concluded that the formation of SA could be induced by salt stress. Exogenous SA treatment could induce an increase in H$_2$O$_2$ levels in plant tissues. In maize plants, pretreatment with SA or aspirin activated some antioxidant enzymes (peroxidase and GR), which in turn increased chilling tolerance (Janda et al. 1999, 2000). Kang et al. (2003) reported that banana (Musa acuminate) treated with 0.5 mM SA at 30/22°C for 1 d did not change (SOD) activity. A chilling stress of 3 d at 5°C quickly reduced SOD activity both in control and SA pretreated plants. SOD activity in leaves of SA pretreated seedling was significantly higher than in the control plants. At 30/22°C, SA treatment for 1 d markedly inhibited CAT and APX activities. A chilling stress of 3 d at 5°C caused a rapid decrease of CAT and peroxidase activities in leaves of control plants; while it significantly induced an increase in the activities of CAT and APX in SA pretreated leaves. Changes in the enzyme activities such as SOD and H$_2$O$_2$ degrading enzymes such as CAT, APX and peroxidase induced by SA treatment resulted in the difference of H$_2$O$_2$ levels. In Arabidopsis, SA was found necessary for the induction of antioxidative defenses and maintaining the redox state of glutathione (GSH) pool (Sharma et al. 1996). Thus, SA has been shown to be essential for carbon uptake or fixation of Rubisco enzyme and antioxidative stress generated by ozone (Rao and Davis 1999).

Szepesi et al. (2005) reported that SA pretreatment decreased CAT activity in the roots and leaves of tomato, but the activity of other enzymes associated with the antioxidative defense, SOD, peroxidase, APX and GR exhibited different changes at 10$^{-3}$ M SA or 10$^{-4}$ M SA. The activity of all these enzymes decreased compared to the control in the absence of SA as concentration of SA increased. At 10$^{-3}$ M concentration their activity was enhanced. Salt tolerance induced by 10$^{-3}$ M SA was associated with the activation of the oxidative defense mechanisms and with the accumulation of osmolytes. Wang and Li (2006) noticed that exogenous SA pretreatment decreased thiobarbituric acid reactive substances (TBARS) and relative electrolyte leakage in grape (Vitis vinifera) leaves under heat or cold stress. Exogenous SA pretreatment induced threer, white rice, while it maintained relatively higher activities of APX, GR, monodehydroascorbate (MDHA) and the redox ratio in the ascorbate glutathione (AsA-GSH) pool under normal temperature and under heat or cold stress. Cytosolic Ca$^{2+}$ in SA-treated mesophyll cells was greater than that in controls at the normal temperature. SA treated cells maintained Ca$^{2+}$ homeostasis under cold or heat stress and increased tolerance.
CONCLUSIONS

The literature reviewed above includes few reports concerning the effect of SA on the physiological processes and the productivity of important crop species under salinity stress. Further, our understanding on the response of SA in enhancing/strengthening tolerance of plants and alleviating the effects of salinity stress in economically important crop plants requires more experimentation and studies. Studies have strengthened postulations that SA acts as signaling molecule affecting several physiological and biochemical processes under different abiotic stress conditions. It is, therefore necessary to have in-depth study on the molecular mechanisms of SA-mediated tolerance. As the effects of SA are concentration dependent, it would be worthwhile to investigate the possible explanations for the differential response of plant tissues to SA.

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