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Physiological Aspects of Salicylic Acid-Mediated Salinity Tolerance in Plants

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ABSTRACT

Salicylic acid (SA) has been known to present in plant tissues for quite some time, but has only recently been recognized as a potential plant growth regulator. Studies indicate the significant role of SA in the signal transduction pathway of biotic stresses in plants. The application of exogenous SA could provide protection against several types of abiotic stresses such as, salinity, high or low temperature, heavy metals, etc. Although SA may also cause oxidative stress to plants, partially through the accumulation of hydrogen peroxide, the results published so far show that the preliminary treatment of plants with low concentrations of SA might have acclimation-like effects. Such acclimation effect is associated with several physiological processes. The present mini-review explores the available information in the literature on the physiological aspects of SA-mediated salinity tolerance.

Keywords: oxidative stress, salicylic acid, salinity stress tolerance

Abbreviations: BA, benzoic acid; **CA**, *trans*-cinnamic acid; **PGR**, plant growth regulator; **SA**, salicylic acid; **t-PAL**, phenylalanine ammonia lyase

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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 Saidi 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 Kazlauskienė 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

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grouped into cellular homeostasis (including ion homeostasis and osmotic adjustment) or stress damage control (repair and detoxification and growth regulation) (Hirt and Shinozaki 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 under 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.

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, transpiration, ion uptake and transport and also induces specific changes in leaf anatomy and chloroplast structure. Considerable interests have been aroused by the ability of SA to produce a protective effect on plants against various stress factors of different abiotic nature. Thus, convincing data have been obtained concerning the SA-induced increase in the resistance of wheat seedlings to salinity (Sakhabutdinova *et al*. 2003), and water deficit (Bezrukova *et al*. 2001), of tomato (*Lycopersicon esculentum*) and bean (*Phaseolus aureus*) plants to low and high temperature (Senaratna *et al*. 2000), as well as the injurious action of heavy metals on rice (*Oryza sativa*) plants (Choudhury and Panda 2004). Application of SA has been reported to increase heat tolerance in creeping bent grass (*Agrostis palustris*) (Larkindale and Huang 2004) and tall fescue (*Festuca arundinacea*) seedlings (He *et al*. 2002). Improved heat tolerance in creeping bent grass by application of SA was associated with its protection against oxidative damages (Larkindale and Huang 2004). SA improves heat tolerance of chickpea (*Cicer arietinum*) to high temperature stress (Chakraborty and Tongden 2005). Keeping in view the attention focused on SA in recent years as phytohormones and its effect on various aspects of physiological, biochemical and metabolic characteristics, the present mini-review thus, aimed at exploring the available data and/or literature on SA-mediated amelioration of salinity stress.

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 cinnamic acid catalysed by PAL has been acknowledged as the rate-limiting step in the *de novo* biosynthesis of SA (Coquoz *et al*. 1998). Special attention has been paid to the BA2H (benzoic acid 2-hydrozylase) enzyme, which displays its biochemical function in the hydrozylation of BA to SA. Dat *et al*. (1998) found that both free SA and total SA levels were elevated during the first 30 min following heat acclimation. Their results indicated that the rapid increase in free SA content, for the most part, could be attributed to the biosynthesis of SA, with the final step catalyzed by BA2H. Glucosylation is a common modification of plant secondary metabolites (Jones and Vogt 2001; Claire *et al*. 2005). Dean *et al*. (2003) found that SA was converted to SAG (Salicylic acid β-glucoside) in cytoplasm catalysed by the SAGT (Salicylic acid glucosyltransferase) enzyme, with the resulting newly formed SAG-stored in the vacuole. Benzoic acid hydrozylase (BA2H), whose major biochemical function is catalyzing the conversion of BA to SA, has received increased attention in the regulation of SA biosynthesis and physiological processes related to SA signaling. Several research groups have reported that BA hydroxylation to SA appears to be the final and rate-limiting step in SA biosynthesis (Leon *et al*. 1995; Coquoz *et al*. 1998; Ribnicky *et al*. 1998) (**Fig. 1**).

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*. 1994; Szalai *et al*. 2000). 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 an important role in flower induction, growth and development, ethylene biosynthesis, stomatal behaviour and respiration (Raskin 1992). It is important in disease resistance (Raskin 1992; Klessig and Malamy 1994) but the exact mode of the action of SA in this direction is not known. The application of 0.5 mM SA substantially reduced the negative effects of salt stress on growth, photosynthetic and yield traits in mungbean (*Vigna radiata*) through increasing 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-

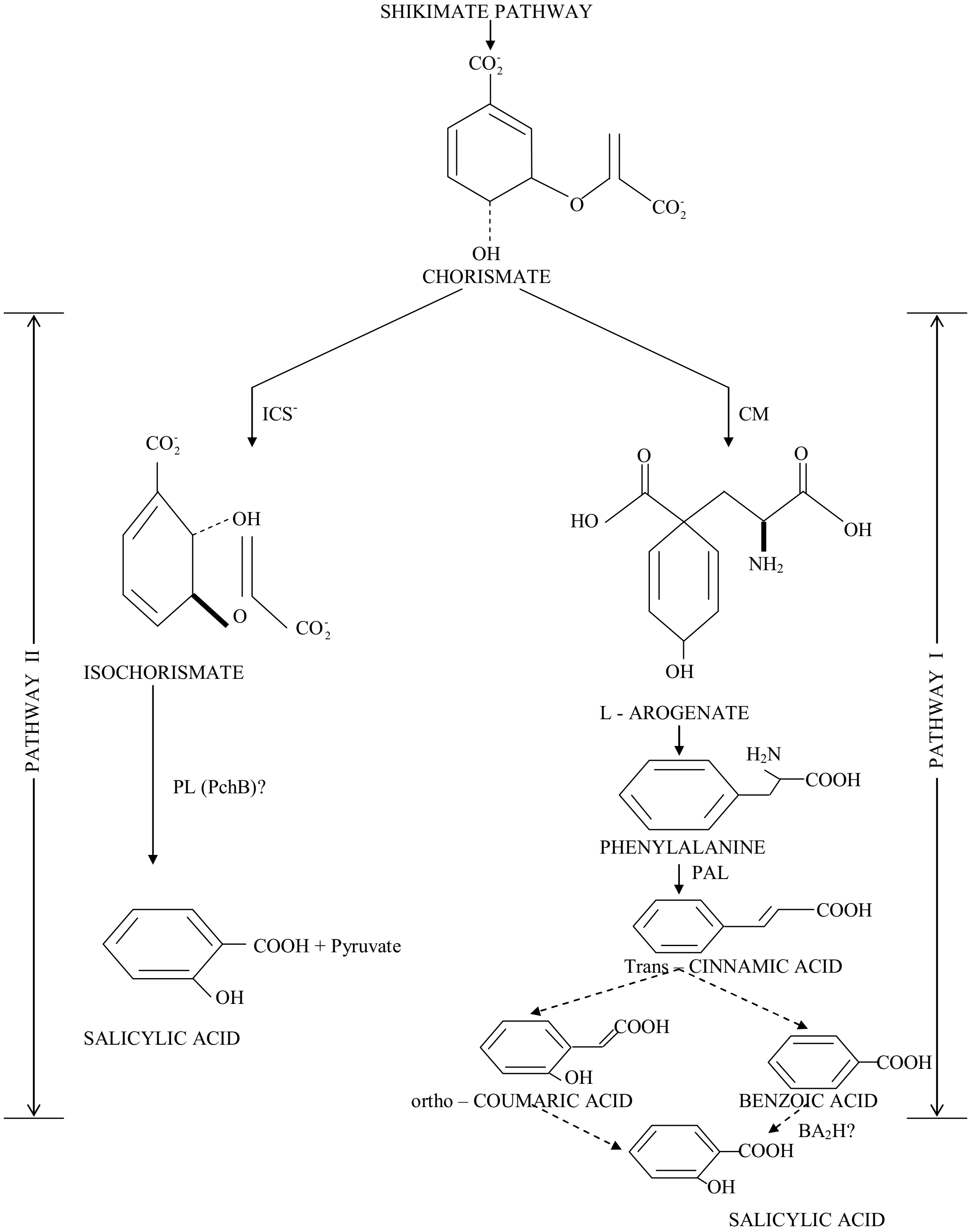

Fig. 1 Proposed pathways of salicylic acid (SA) biosynthesis in plants. After: Yalpani *et al.* (1993) and van Tegelen *et al.* (1999). Abbreviations: **ICS**, isochorismate synthase; **CM**, chorismate mutase; **PAL**, phenylalanine ammonia lyase; **BA2H**, benzoic acid 2–hydroxylase; **PL(PchB)**, pyruvate lyase.

teristics 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 quenching of excess excitation energy (Gilmore and Yamamoto 1993). The size of xanthophylls has been found increased in plants grown under stress conditions (Demmig-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; Amaresh-Chandra *et al.* 2001; Guleria *et al.* 2001; Negi and Prasad 2001; Vasudha *et al.* 2001). In addition, several attempts have been made to induce resistance by increasing endogenous SA level in plants.

Keshamma *et al.* (2004) reported the effect of SA on germination of chickpea seeds. Seeds treated with water and 1 mM SA concentration started to germinate on 1 d of sowing while seeds treated with SA at 2, 3 and 4 mM concentrations started to germinate on 2, 3 and 4 d, respectively. However, at 5 mM concentrations no seeds were germinated even after 5 d of sowing. An exogenous supply of SA affects seedling growth and/or seed germination. Higher concentrations of SA decreased the germination process in soybean (*Glycine max*) seeds (Negi and Prasad 2001). Convincing data are available concerning the SA-induced increase in the resistance of wheat seedlings to salinity (Shakirova and Bezrukova 1997), and water deficit (Bezrukova *et al.* 2001) of tomato and bean plants to low and high temperature (Senaratna *et al.* 2000), as well as the injurious action of heavy metals on rice plants (Mishra and Choudhuri 1999).

The important role of SA in the protection against stress in *Arabidopsis* is probably played by its ability to induce expression of genes coding not only for proteins but also extends in gene in *Arabidopsis* plants (Merkouropoulos *et al.* 1999). There are convincing data about SA-induced synthesis of heat shock proteins in tobacco (*Nicotiana tobacum*) plants (Burkhanova *et al.* 1999) and the accumulation of lectins in wheat (Shakirova and Bezrukova 1997), fast activation of 48 kDa protein kinase in suspension cell culture of tobacco at osmotic stress (Mikolajczyk *et al.* 2000). This suggested the involvement of SA in realization of different anti stress programs. However, the way of signal regulation of plant resistance to unfavorable factors of environment induced by SA is still not well understood.

Pre-sowing treatment of wheat seeds with SA contributed to the increase in the resistance of plants to stress factors of environment and abscisic acid (ABA) served as a mediator in the manifestation of the protective action of SA. SA treatment induced a sharp accumulation of ABA, which in turn is an inducer of a wide spectrum of anti stress reactions in plants. Maintaining a high level of ABA in SA-treated plants under stress contributed to the protective reactions aimed to decrease its injurious effects on growth and acceleration of growth resumption. Several studies have supported a major role of SA in the modulation of the plant responses to several abiotic stresses, such as ultraviolet light, drought, salt, chilling and heat (Yalpani *et al.* 1994; Dat *et al.* 1998a, 1998b; Janda *et al.* 1999; Mishra and Choudhuri 1999; Senaratna *et al.* 2000). In maize (*Zea mays*) plants, pretreatment with SA or aspirin caused a decrease in net photosynthesis under normal growth conditions (Janda *et al.* 1999, 2000).

Popova *et al.* (2003) reported that treatment of barley seedlings with SA in the dark followed by 6 h light exposure did not cause wilting or irreversible damage to photosynthesis. Concentrations of SA are very relevant for physiological studies. They did not observed visible damage symptoms after long-term treatment, but provided well-reproducible and reversible effects on photosynthesis, growth and biochemistry of barley plants. Treatment of barley seedlings with SA caused an inhibition in the net photosynthetic rate. Dark-treated barley seedlings with SA did not show loss in chlorophyll content. Pretreatment of plants with SA before paraquat application caused a protection against paraquat-induced Chl losses. No significant changes in the protein levels were observed in SA and dark-treated seedlings. Pretreatment with SA before paraquat prevented the protein loss RuBPC (ribulose-1,5-biphosphate carboxylase) activity was almost unaffected when plants were treated with SA (Popova *et al.* 2003). Pretreatment with SA before application of paraquat had no effect on the enzyme activity.

Several studies carried out under laboratory or field conditions strongly suggest that SA and other salicylates play an important role in many biological responses in plants. The effect of these substances on the physiology 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 (Nemeth *et al.* 2002).

Szepesi *et al.* (2005) reported that the 10^{-7} M SA pretreatment in tomato decreased the osmotic stress-induced reduction in relative water content, but this alleviating effect was not so pronounced at 10^{-4} 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 greatly decreased and the SA pretreatments moderated it at both 10^{-7} M and 10^{-4} 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 μmol 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 exogenously 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_2O_2 concentration were increased by increasing levels of SA. SA also strongly inhibited Na^+ and Cl^- accumulation (as also observed in authors laboratory in mungbean, the effects of 50 mM NaCl were reversed with the application of 0.5 mM SA. 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-indused stomatal closure (Noreen and Ashraf 2008). However, it can be suggested that foliar spray with SA might 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, Kovacik *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 antioxidant system. SA has been reported to influence the activities of antioxidative enzymes differentially. In general, authors found enhancement in the activities of antioxidant enzymes such as, superoxide dismutase (SOD), glutathione reductase (GR) and ascorbate peroxidase (APX) with NaCl and 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 control (unpublished data). The increases in the activities of antioxidant enzymes following SA application could be the indicator of build-up of a protective mechanism against oxidative damage induced by salt stress through increase in nutrients contents and antioxidative metabolism (Khan *et al.* 2010). Gunes *et al.* (2007) have reported that exogenously applied SA involved in the induction of at least one of cellular mechanisms that are concomitant with the accumulation of active oxygen species (AOS). It was found that inhibition of catalase, a H_2O_2 scavenging enzyme, by SA plays a major role in the generation of ROS (Horvath *et al.* 2007). SA inhibited the activities of catalase (CAT) and APX and increased the content of H_2O_2 (Chen *et al.* 1993; Durner and Klessig 1995; Rao *et al.* 1997; Kawano and Muto 2000; Luo *et al.* 2001). Moharekar *et al.* (2003) suggested that an increase in SA concentration might induce oxidative stress in wheat and mungbean but the degree of oxidative stress was different in different plant species. CAT activity from cucumber (*Cucumis sativus*), tomato, *Arabidopsis* and tobacco has been found substantially inhibited by SA, whereas those from maize and rice were found to be insensitive (Sanchez-Casas and Klessig 1994). In contrast, Keshamma *et al.* (2004) found that CAT activity in roots of chickpea was not inhibited by SA *in vitro*. At 200 mM NaCl concentration only 30% inhibition was observed. However, when seeds were soaked at different time intervals in 1 mM SA, there was a complete inhibition of CAT activity. The treatment of SA + spermine enhanced total guaicol peroxidase activity by about 20- and 100-fold in seeds and roots, respectively compared to control.

Stimulation or inhibition in the activities of peroxidase, PAL by SA has been reported to be concentration dependent (Jain and Srivastava 1981a, 1981b). It has been reported that SA increased peroxidase, PAL activities by inducing 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 SA content in the NaCl-treated leaves 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_2O_2 levels in plant tissues. In maize plants, pretreatment with SA or aspirin activated some antioxident enzymes (peroxidase and GR), which in turn increased chilling tolerance (Janda *et al.* 1999, 2000). Kang *et al.* (2003) reported that banana (*Musa acuminata*) 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_2O_2 degrading enzymes such as CAT, APX and peroxidase induced by SA treatment resulted in the difference of H_2O_2 levels. In *Arabidopsis*, SA was found necessary for the induction of antioxidant defenses and maintaining the redox state of glutathione (GSH) pool (Sharma *et al.* 1996). Thus, SA has been shown to be essential for the plant protection against the oxidative 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^{-7} M SA or 10^{-4} M SA. The activity of these enzymes decreased compared to the control in the leaves of tomato plants at 10^{-7} M SA pretreatment, while at 10^{-4} M concentration their activity was enhanced. Salt tolerance induced by 10^{-4} 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 enabled the grape leaves to maintain 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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