J Plant Growth Regul (2007) 26:290–300
DOI 10.1007/s00344-007-9017-4

REVIEW

Induction of Abiotic Stress Tolerance by Salicylic Acid Signaling

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Received: 8 December 2006 / Accepted: 14 February 2007 / Published online: 21 August 2007

Abstract The role of salicylic acid (SA) as a key molecule in the signal transduction pathway of biotic stress responses has already been well described. Recent studies indicate that it also participates in the signaling of abiotic stresses. The application of exogenous SA could provide protection against several types of stresses such as high or low temperature, heavy metals, and so on. 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 an acclimation-like effect, causing enhanced tolerance toward most kinds of abiotic stresses due primarily to enhanced antioxidative capacity. The effect of exogenous SA depends on numerous factors such as the species and developmental stage of the plant, the mode of application, and the concentration of SA and its endogenous level in the given plant. Recent results show that not only does exogenous SA application moderate stress effects, but abiotic stress factors may also alter the endogenous SA levels in the plant cells. This review compares the roles of SA during different abiotic stresses.

Keywords Abiotic stress · Antioxidant enzymes · Hydrogen peroxide · Oxidative stress · Reactive oxygen species · Salicylic acid

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Introduction

Salicylic acid (SA) has long been known as a signal molecule in the induction of defense mechanisms in plants (Raskin 1992; Klessig and others 2000; Shah 2003; Halim and others 2006). In higher plants SA derives from the shikimate-phenylpropanoid pathway (Sticher and others 1997). Two routes of synthesis that differ at the hydroxylation of the aromatic ring have been described. Phenylalanine is converted into cinnamic acid (CA). Then CA can be (1) hydroxylated to form o-coumaric acid followed by oxidation of the side chain or (2) the side chain of CA is initially oxidized to give benzoic acid which is then hydroxylated in the ortho position. There is a third way for SA to be biosynthesized from shikimic acid via chorismic and isochorismic acid, which was originally described in bacteria but has recently been shown to take place in the chloroplast in plants (Wildermuth and others 2001; Wildermuth 2006).

Experiments on transgenic plants in which the synthesis and metabolism of SA was altered showed that its presence is needed for the development of stress symptoms and hypersensitive-response (HR)-like cell death. Exogenous SA treatment may also induce the expression of pathogenesis-related (PR) proteins (Malamy and others 1990) and establish systemic acquired resistance (SAR) (Métraux and others 1990; Gaffney and others 1993). Although SA is not considered to be the signal translocated from the infection site, its accumulation in distant tissues is essential for the induction of SAR (Vernooij and others 1994). It must also be stressed that the mode of action of SA in the induction of biotic stress tolerance may vary with species, especially when dicot and monocot plants are compared (Kogel and Langen 2005).

SA was also shown to influence a number of physiologic processes (Raskin 1992). It increases the expression of alternative oxidase (Rhoads and McIntosh 1992), thus enhancing cyanide-resistant respiration. It may also uncouple the mitochondrial electron transport chain (Norman and others 2004), or may induce heat production, which is also due to the enhanced activity of the cyanide-resistant or alternative respiration chain (Raskin and others 1987). An increase in the alternative pathway can also be observed under stress conditions in plants, as described for chilling stress (Moynihan and others 1995). Wheat seedlings soaked in SA solution possessed significantly higher leaf number, biomass production, and nitrate reductase and carbonic anhydrase activities than untreated plants (Hayat and others 2005).

Because several of the processes related to the action of SA are not specific to any given stress factors, it seemed logical that SA might have a role not only in biotic but also in abiotic stresses. Some experiments have studied the effect of exogenous SA on the abiotic stress tolerance of plants, or vice versa, the effect of abiotic stresses on the endogenous SA level. To study the involvement of SA in abiotic stress responses, either the SA-deficient transgenic plants expressing a bacterial salicylate hydroxylase (*NahG*) that degrades SA to catechol or mutant plants defective in SA perception or SA production were used by several authors. Some of these mutants, for example, *cep* (constitutive expression of *PR-1* gene), express *PR* genes and accumulate high levels of SA. Because of the high SA level in these mutants, the corresponding genes probably encode components that function upstream of SA, or they may encode components of a separate pathway that impinges on the SA pathway (Klessig and others 2000). By contrast, the mutant *eds5* has a mutation upstream of SA and, similar to the *sid2* (SA-induction deficient) mutant, is characterized by low SA levels and enhanced disease susceptibility (Rogers and Ausubel 1997). One of the most frequently used mutants is the *npr1* mutant (nonexpresser of *PR* genes), which fails to express *PR* genes and exhibits enhanced disease susceptibility even after SA treatment (Cao and others 1994).

Connection Between Biotic and Abiotic Stresses

Ultraviolet light and ozone exposure both induced SA accumulation, PR protein expression, and virus resistance in tobacco (Yalpani and others 1994). The role of SA in the defense against ozone stress was also demonstrated in *Arabidopsis thaliana* plants (Sharma and others 1996), because the SA-deficient *NahG* transgenic line proved to be more sensitive to ozone exposure. SA was shown to be required for the induction of ozone-induced mRNAs. According to these experiments *Arabidopsis thaliana* plants exposed to ozone exhibited increased resistance to infection with virulent phytopathogenic *Pseudomonas syringae* strains. These results indicate that the pathways of ozone- and pathogen-induced resistance overlap and are both SA-dependent. The induction of antioxidant defenses by ozone stress was also proven to be dependent on SA, because it was significantly impaired in *NahG* plants (Rao and Davis 1999). On the other hand, the highly ozone-sensitive *Arabidopsis thaliana* genotype Cvi-0 accumulated a higher level of SA, which in turn induced HR-like cell death by initiating an oxidative burst (Rao and others 2000). Exogenously applied SA also increased the O_3 sensitivity of *Arabidopsis* plants (Rao and others 2002). Thus, as also shown in several other examples, the concentration of SA seems to be crucial in the regulation of stress responses.

The overexpression of the pepper basic *PR1* gene in *Arabidopsis* confers not only enhanced resistance to *Pseudomonas syringae*, but also enhanced tolerance to oxidative stress caused by methyl viologen and to ionic and nonionic osmotic stresses (Hong and Hwang 2005). Simulated acid rain causes leaf necrosis in *Arabidopsis* and increases the expression of genes in the SA-mediated pathogen resistance pathway (Lee and others 2006). *NahG* transgenic *Arabidopsis* plants, which cannot accumulate SA, were more sensitive to simulated acid rain and displayed more intensive necrosis than wild-type plants. These results suggest that the SA-dependent signaling pathway is involved not only in the induction of systemic acquired resistance but is also activated by the simulated acid rain and has a role in protection against its damaging effects.

Protection by SA Against Abiotic Stress Factors

Toxic Metals In one of the first works demonstrating the protective effect of SA against an abiotic stress factor, SA treatment induced tolerance against copper toxicity in cucumber and tobacco (Strobel and Kuc 1995), and, as was shown later, in sunflower plants (El-Tayeb and others 2006). SA treatment was also shown to have an ameliorating effect on seed germination and seedling growth under Pb^{2+} or Hg^{2+} stresses in two rice plants (Mishra and Choudhuri 1997). Pretreatment of barley seedlings with SA prevented the lipid peroxidation caused by Cd and increased shoot and root fresh weight. This protection was not, however, the consequence of an upregulation of antioxidant activity. On the other hand, antioxidant enzyme activities were found to increase in Cd-stressed seedlings, but pretreatment with SA suppressed this effect (Metwally and others 2003). In soybean (*Glycine max* L. cv SG1) seedlings simultaneously treated with SA and Cd, SA concentrations of 10^{-6}, 10^{-5}, and 10^{-4} M alleviated the effects of Cd, for example, growth inhibition, desiccation, and decrease in chlorophyll content (Drazic and Mihailovic 2005). Although SA did not decrease the Cd uptake in soybean, it did change its distribution in plant organs. In alfalfa (*Medicago sativa* L. cv Evropa), the imbibition of 10^{-5} M SA caused an increase in the Cd uptake of the seeds (Drazic and others 2006). In the case of maize, although exogenous SA application (added to the hydroponic solution) reduced the uptake of Cd by the roots, SA itself caused oxidative stress to the plants, thereby aggravating the symptoms of cadmium stress (Pál and others 2002). However, when maize seeds were presoaked in SA solution for 6 h before germination, this treatment significantly reduced the damaging effect of Cd on the photosynthetic processes (Krantev and others 2007). In *Cassia tora* L. plants, SA enhanced Al tolerance by increasing the citrate efflux of the roots and thus inhibiting Al uptake (Yang and others 2003). Al was also shown to increase the SA concentration of the roots. Cd treatment increased the endogenous free SA content in barley (Metwally and others 2003) and in maize (Pál and others 2005).

Heat Stress

The first paper to demonstrate the effect of SA on heat tolerance showed that the heat tolerance of mustard plants was improved by spraying with SA (Dat and others 1998a). This effect was concentration-dependent, as SA exhibited a protective effect only at low concentrations (0.01–0.1 mM). Both treatment with 0.01 mM SA and hardening at 45°C for 1 h led to an increase in the H_2O_2 level and a reduction in catalase activity. It also enhanced the thermotolerance of tobacco plants when applied at low concentration (10 µmol/L), whereas at ten times this concentration it had no protective effect against heat stress (Dat and others 2000). Not only heat acclimation but also the application of exogenous SA improved the survival of pea plants after heat stress. The direct role of SA synthesis in heat acclimation was proven using inhibitors of SA synthesis, which reduced not only the endogenous SA content, but also the level of heat tolerance (Pan and others 2006). In cucumber plants (*Cucumis sativa* L.), foliar spraying with 1 mM SA induced heat tolerance, as shown by the lower electrolyte leakage parameter, lower H_2O_2 and lipid peroxide levels, and higher Fv/Fm chlorophyll *a* fluorescence value, whereas the hydroponic application of the same concentration had the opposite effect (Shi and others 2006). Catalase activity seems to be crucial for the removal of H_2O_2 during heat stress, as it was found to be enhanced by the foliar application of SA but inhibited in the hydroponically treated plants. Acetyl-SA also proved to be effective in inducing thermotolerance in potato microplants (Lopez-Delgado and others 1998). SA was shown to play a role in the induction of thermotolerance in *Arabidopsis* plants (Larkindale and Knight 2002). Plants may also tolerate elevated temperatures without heat acclimation or any chemical treatment. This phenomenon is called basal thermotolerance. Plants subjected to mild heat stress may transiently acquire tolerance to previously lethal high temperatures (that is, heat acclimatization or acquired thermotolerance) (Clarke and others 2004). Screening *Arabidopsis* mutants and *NahG* transgenic plants for their basal and acquired thermotolerance showed that ABA, ROS, and SA play a role in the development of acquired thermotolerance (Larkindale and others 2005). However, in another experiment on *Arabidopsis* plants, SA was shown to be essential for basal but not for acquired thermotolerance (Clarke and others 2004). As a further proof of the role of SA in heat tolerance, the endogenous bound and free SA levels were found to increase during heat acclimation of mustard seedlings (Dat and others 1998b). The level of SA was shown to increase slightly after the first hour of heat stress in creeping bentgrass (*Agrostis stolonifera*) (Larkindale and Huang 2005). Heat acclimation was also followed by a transient increase in the endogenous SA level in pea (*Pisum sativum* L.) plants, whereas inhibitors of SA biosynthesis reduced the tolerance of the plants to heat stress (Pan and others 2006). Experiments on grapevine (*Vitis vinifera* L.) also showed a sharp increase in the SA level at the beginning of heat acclimation, whereas exogenous SA also induced a level of thermotolerance similar to that of heat acclimation (Wang and Li 2006). This induction of thermotolerance was related to changes in the antioxidant enzyme activities.

Low Temperature

Tolerance against low, nonfreezing temperatures is an important trait of plants of tropical or subtropical origin. Irrespective of its mode of application, exogenous SA was shown to enhance the chilling tolerance of various species. SA and other phenolic compounds (benzoic acid, acetyl-SA, and so on) increased the chilling tolerance of young maize plants when applied hydroponically at a concentration of 0.5 mM (Janda and others 1999, 2000; Horváth and others 2002). This enhanced tolerance was accompanied by increased activities of glutathione reductase and guaiacol peroxidase and a decrease in catalase. In maize, rice, and cucumber, hydroponic SA treatment increased the chilling tolerance of the shoots but not of the roots (Kang and Saltveit 2002), and it was accompanied by an increase in the glutathione reductase and guaiacol peroxidase activities in the shoots. Pretreatment of potato plants with 0.1 mM

SA also induced chilling tolerance (Mora-Herrera and others 2005). In banana seedlings (*Musa acuminata*), 0.5 mM SA solution induced chilling tolerance both when sprayed onto the leaves and applied in irrigation to the roots (Kang and others 2003). At a normal growth temperature of 30/22°C, the H_2O_2 level of banana plants increased after SA treatment. However, at 5°C the SA treatment decreased the H_2O_2 level and activated the superoxide dismutase, catalase, and ascorbate peroxidase enzymes. Recent results show that SA may alleviate chilling injury not only at the whole-plant level but also when only the fruits are treated. When tomato plants were treated with 0.01 mM methyl salicylate and methyl jasmonate, the cold tolerance of the fruits increased and PR protein expression was induced (Ding and others 2002). Higher concentrations (0.1 and 0.5 mM), however, tended to decrease cold tolerance. Similar results were shown for peaches treated with SA and stored at low temperatures (Wang and others 2006).

In chilling-resistant *Arabidopsis* plants, SA was shown to accumulate during cold treatment at 5°C (Scott and others 2004). *Arabidopsis* plants have restricted growth at this temperature, and the higher level of SA might mediate this growth inhibition because SA-deficient *NahG* plants showed a higher growth rate than wild-type plants.

The effect of SA is not as clear for freezing tolerance of plants as for cold tolerance. Winter rye leaves accumulated apoplastic proteins without antifreeze activity when sprayed with SA, whereas ethylene treatment caused an increase in antifreeze activity (Yu and others 2001). Cold acclimation and drought acclimation both resulted in an increase in ethylene production and antifreeze activity. These results suggest that the induction of freezing tolerance is mediated by ethylene but not by SA. On the other hand, other results showed that SA spraying enhanced the freezing tolerance of wheat because the ice nucleation activity of apoplastic proteins increased after SA treatment (Tasgín and others 2003, 2006).

Osmotic and Salt Stress

In the case of salt stress and osmotic stress, the effect of SA is rather ambiguous. SA was shown to potentiate the generation of reactive oxygen species (ROS) in photosynthetic tissues of *Arabidopsis thaliana* during salt and osmotic stresses, thus participating in the development of stress symptoms (Borsani and others 2001). After NaCl (100 mM) or mannitol (270 mM) treatment, SA-deficient *NahG* plants did not show the extensive necrosis in the shoots observed in wild-type plants. However, when applied exogenously by soaking barley grains in 1 mM SA before sowing, it increased the tolerance of the plants to salt stress (El-Tayeb 2005). The application of 0.05 mM SA also improved plant growth after salt stress and caused the accumulation of ABA and prolines (Shakirova and others 2003). SA added to the soil also had an ameliorating effect on the survival of maize plants during salt stress and decreased the Na^+ and Cl^- accumulation (Gunes and others 2007). Lipid peroxidation and membrane permeability, which were increased by salt stress, were lower in SA-treated plants. SA treatment was accompanied by a transient increase in the H_2O_2 level. As seed treatment with H_2O_2 itself had an alleviating effect on the oxidative damage caused by salt stress in wheat plants (Wahid and others 2007), it seems possible that SA may exert its protective effect partially through the transiently increased level of H_2O_2. Root drenching with 0.1 mM SA protected tomato (*Lycopersicon esculentum*) plants against 200 mM NaCl stress (Stevens and others 2006). It increased the growth and photosynthetic rate of the plants, as well as the transpiration rate and stomatal conductance, and reduced electrolyte leakage by 32%. The endogenous level of SA increased under salt stress in rice seedlings and the activity of the SA biosynthesis enzyme, benzoic acid 2-hydroxylase, was induced (Sawada and others 2006). The effect of salinity on the endogenous concentration of various phytohormones was investigated in *Iris hexagona* (Wang and others 2001), and the levels of ABA and JA were generally found to increase, although, interestingly enough, SA declined in response to salinity.

The improving effect of SA is not always obvious with respect to drought tolerance of plants. Pretreatment of 2-week-old maize plants with 0.5 mM SA for 1 day decreased their drought tolerance, although it increased the polyamine content of the plants (Németh and others 2002). However, when SA was applied by soaking the grains before sowing, it improved the drought tolerance of plants. Soaking wheat grains with 100 ppm acetyl-SA had an alleviating effect on the injury of plants subjected to drought stress (Hamada 1998; Al-Hakimi and Hamada 2001). In the case of tomato and bean plants, 0.1 and 0.5 mM SA or acetyl-SA increased drought tolerance when imbibed by the seeds for 1 day or when applied to 2-week-old plants by soil drenching 1 week before drought stress (Senaratna and others 2000). In wheat seedlings SA treatment resulted in higher moisture content, dry mass, carboxylase activity of Rubisco, superoxide dismutase activity, and total chlorophyll content during drought stress compared to untreated seedlings (Singh and Usha 2003). Drought stress may also be accompanied by oxidative stress (Czövek and others 2006; El-Tayeb 2006). Spraying wheat leaves with 1 mM SA increased antioxidant enzyme activities, chlorophyll and relative water content, and the membrane stability index, and decreased H_2O_2 and lipid peroxide levels under moderate water stress (Agarwal and others 2005). Treatment of plants with SA before stress reduced the damaging action of water deficit on cell membranes and increased the ABA content in barley leaves (Bandurska and Stroinski 2005). The endogenous SA content in leaves of *Phillyrea angustifolia* L. plants increased progressively up to fivefold during drought (Munne-Bosch and Penuelas 2003). During recovery, the SA levels decreased but remained slightly higher than those observed before drought. Water deficit increased the SA content in the roots of barley plants, whereas the SA content in the leaves did not change (Bandurska and Stroinski 2005).

Direct Oxidative Damage

Because of the imbalance in the cellular machinery leading to the accumulation of harmful ROS, the majority of stress factors discussed above may also be related to oxidative damage. The most obvious sign of the presence of oxidative stress accompanying other abiotic stress factors is an increased amount of lipid peroxides, which may cause the death of the cells. Certain compounds may directly induce oxidative stress. In a few experiments SA was found to be an effective preventive agent against these compounds. Pretreatment by spraying cucumber and tobacco leaves with NaSA can protect them from oxidative stress induced by paraquat applied 3 days after the SA pretreatment (Strobel and Kuc 1995). Similarly, pretreatment of barley seedlings with SA in the dark via the transpiration stream fully blocked the subsequent light-induced inhibitory effect of paraquat on photosynthesis and also decreased the paraquat-induced production of H_2O_2, lipid peroxidation, and electrolyte leakage (Ananieva and others 2002), while inducing the activities of certain antioxidant enzymes (Ananieva and others 2004). Recently, these results were confirmed using SA-deficient *NahG* transgenic rice plants, which showed great sensitivity to paraquat. These plants also had lower glutathione content, which may explain the greater sensitivity of these plants to oxidative damage and also suggests that SA may regulate glutathione synthesis in rice (Kusumi and others 2006).

Possible Mechanisms

These results indicate that SA is involved in the abiotic stress responses of plants. It participates in the development of stress symptoms, but it is also needed for the acclimation process and the induction of stress tolerance. *NahG* plants seemed to be more tolerant in some cases, as necrotic lesions did not appear on them (Borsani and others 2001), although in other cases they were more susceptible to ozone exposure, as the induction of acclimation was defective. Most abiotic stresses increased the *in planta* concentration of SA, which also points to its involvement in stress signaling. The effect of exogenous SA on the stress tolerance of plants is not always obvious. It depends not only on the applied concentration and the mode of application, but also on the overall state of the plant: developmental stage, oxidative balance of the cells, and acclimation by previous biotic or abiotic stresses.

Effect of SA on the Oxidative Status of Plants

As already shown above, the application of exogenous SA may provide protection against direct oxidative damage in plants. In contrast to the majority of plants tested so far, rice has an exceptionally high basal free SA level, far exceeding the elevated SA levels in infected tobacco or *Arabidopsis* tissues. This SA level hardly changed after pathogen infection, and rice plants seem to be insensitive to exogenous SA application. SA-deficient *NahG* transgenic rice plants were hypersensitive to oxidative damage caused by paraquat treatment (Yang and others 2004). These experiments show a direct role of endogenous SA in the regulation of the redox balance and in protecting rice plants from oxidative damage. However, exogenous SA application itself may also cause oxidative stress to plants. At relatively low concentrations (0.05–0.5 mM) it acts as a moderate stress, having an effect on the oxidative status of the plant similar to that of stress-acclimating processes. A rapid transient increase in ROS is followed by enhanced antioxidative capacity, which protects the plant from the severe damage caused by subsequent abiotic stress factors. Higher concentrations of SA cause a level of oxidative stress that the plant is unable to overcome and which may result in the death of the plant.

SA treatment caused an increase in the H_2O_2 concentration *in vivo*, which is thought to be a signal for the expression of *PR* genes (Chen and others 1993b). In response to SA, H_2O_2 accumulated in the veins of rice plants (Ganesan and Thomas 2001). The resulting overaccumulation of ROS appears to be crucial for the induction of programmed cell death. SA was also shown to cause the *in vitro* inhibition of certain antioxidant enzymes. Glutathione-S-transferase was inhibited *in vitro* by SA in a noncompetitive manner (Watahiki and others 1995). SA was proven to bind directly to the catalase enzyme, inhibiting its activity in tobacco (Chen and others 1993a; Conrath and others 1995) and other plant species (Sánchez-Casas and Klessig 1994; Horváth and others 2002). This inhibition of catalase activity was proposed to explain the increase in H_2O_2 level upon SA treatment and thus to play a role in the onset of SAR (Chen and others 1993b). It was also proven that SA is converted to a free radical during the inhibition of catalase activity and thus induces the accumulation of lipid peroxides (Anderson and others 1998). The lipid peroxidation products were proven to be involved in the induction of PR-1 expression.

SA treatment caused lipid peroxidation, oxidative damage to proteins, and the formation of chlorophyll and carotene isomers in *Arabidopsis* plants. These changes were partly due to the inactivation of the catalase and ascorbate peroxidase enzymes resulting in phytotoxic symptoms (Rao and others 1997). It may also increase the level of H_2O_2 by increasing the activities of Cu/Zn superoxide dismutase. In another experiment, ascorbate peroxidase and catalase were also shown to be downregulated by SA in tobacco plants (Klessig and others 2000). Treatment with H_2O_2 itself, even at a concentration that leads to an *in vivo* H_2O_2 accumulation twice as high as that in leaves treated with SA, did not cause the same rate of damage to membranes and proteins as SA, indicating that the increased H_2O_2 level is not the sole mediator of SA action. However, treatment with dimethylthiourea—a trap for H_2O_2—decreased the effect of SA, thus proving that SA acts partly through H_2O_2 (Rao and others 1997). Similar observations were made in a callus culture of *Astragalus adsurgens* when the effect of 0.15 mM SA on somatic embryogenesis was studied (Luo and others 2001). The SA treatment increased the endogenous H_2O_2 level, which was related to inhibited activities of APX and CAT. Exogenous H_2O_2 treatment nevertheless had a significantly lower impact on somatic embryogenesis than SA, while dimethylthiourea decreased the effect of SA by preventing the accumulation of H_2O_2.

There is also evidence for the H_2O_2-induced accumulation of SA (León and others 1995), leading to the hypothesis of a self-amplifying cycle of SA and H_2O_2, which in turn causes the accumulation of ROS and cell death (Van Camp and others 1998). According to a model describing the induction of programmed cell death and the development of necrotic lesions, SA, ethylene, and H_2O_2 form a self-amplifying cycle and are responsible for the accumulation of ROS and the induction of cell death (Overmyer and others 2003). However, it should also be mentioned that the increase in the H_2O_2 level is not necessarily accompanied by an increase in the SA level. It is widely accepted that SA is involved in HR. However, in the monocot barley plants, the accumulation of H_2O_2 but not SA could be detected during interaction with the powdery mildew fungus (nor did these plants' responses elevate SA content) (Hückelhoven and other 1999).

Protein Kinases

Reversible protein phosphorylation/dephosphorylation plays an important role in signaling adaptive responses to several types of stress. The first step in signal relay is the perception of a chemical or a physical signal, such as a change in temperature or light. One type of sensor commonly used to initiate a response to the signal is a receptor protein kinase (RPK). SA may also regulate the expression of certain RPKs, as described, for example, after wounding in *Brassica oleracea* or in peaches (Pastuglia and others 1997; Bassett and others 2005).

In plants, two classes of stress-activated protein kinases, mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs), have been reported so far to integrate multiple environmental stresses and undergo rapid biochemical activation upon exposure to biotic and abiotic stimulation. The MAPK signal transduction cascades are routes through which eukaryotic cells deliver extracellular messages to the cytosol and nucleus. These signaling pathways direct cell division, cellular differentiation, metabolism, and both biotic and abiotic stress responses. In plants, MAPKs and the upstream components of the cascades are represented by multigene families, organized into different pathways that are stimulated and interact in complex ways. The SA-induced protein kinases may also function as central convergence points in stress signaling in abiotic stresses (Jonak and others 2002).

Calcium may control the activity of plant protein kinases directly or indirectly through calmodulin, a calcium-binding protein. Certain *Arabidopsis* genes encoding a calmodulin-binding protein were shown to be induced by abiotic environmental stresses such as extreme temperatures, UV-B, salt, or wounding, and also by hormones such as ethylene and ABA, and by signal molecules such as methyl jasmonic acid, H_2O_2, and SA (Yang and Poovaiah 2002). The direct interaction of calcium with enzymes implicates a multifamily of proteins referred to as calcium-dependent protein kinases (CDPKs), which fall into the serine/threonine class of protein kinases found mainly in plants. Certain CDPKs from plant species also have been shown to be involved in abiotic stress responses and may also be induced by SA (Chung and others 2004; Leclercq and others 2005). These results indicate that SA may act at least in part as a direct or indirect regulator of the calcium-mediated signal transduction pathways.

Abiotic Stress-specific Genes Induced by SA

The abiotic stress tolerance induced by SA may have various causes. Besides the mechanisms mentioned above, several other genes may also be related to certain kinds of abiotic stress and may also be influenced by SA.

Although abiotic stresses affect plant growth and development, their direct effect on the regulation of the components of the DNA replication machinery is still largely unknown. It was recently shown that not only certain stress factors such as low temperature but phytohormones like SA may also upregulate both topoisomerase genes (Hettiarachchi and others 2005) and a chloroplast elongation factor, which may have an important role in plant adaptation to environmental stresses (Singh and others 2004). Several stress-associated signaling molecules, including ethylene, methyl JA, SA, and 2,4-dichlorophenoxyacetic acid, but not ABA or H_2O_2, are capable of inducing the expression of one of the long terminal repeat retrotransposon families, the TLC1 *in vivo*. This family of retroelements was found transcriptionally active and its expression is induced in response to several stress factors such as wounding or high salt concentrations (Tapia and others 2005). These results suggest that these elements may also take part in the SA-mediated signaling pathways.

Much evidence supports the important but not sole involvement of heat shock proteins (HSPs) in thermotolerance in plants (Clarke and others 2004). The synthesis of these proteins is induced during heat acclimation, and it is proposed that they act as molecular chaperones to protect proteins against irreversible heat-induced damage. The exogenous application of SA at an optimal concentration of 0.1 mM induced the synthesis of Hsp70 and Hsp17.6, which belongs to the class I cytosolic family of small-plant Hsps and has protein-refolding activity, parallel with an increase in the heat tolerance of pea (Pan and other 2006). SA may also influence the Hsp70/Hsc70 expression in tomato cell suspension cultures (Cronje and Bornman 1999). In other cases the effect of SA on Hsp induction is not so obvious. SA has also been reported to induce Hsp17.6 in a concentration-dependent manner in *Arabidopsis* plants, but not Hsp101, which belongs to the Hsp100/ClpB family of ATP-dependent chaperones, thought to disaggregate heat-induced protein complexes (Clarke and others 2004) and has been shown to be essential for thermotolerance in *Arabidopsis* (Queitsch and others 2000). Since it was found that both *NahG* transgenic plants and *npr1* mutants were able to induce Hsp17.6 and Hsp101, it was assumed that SA is essential for basal but not for acquired thermotolerance (Clarke and others 2004). A recently isolated gene, *Oshsp18.0-CII*, has also been shown to be induced by SA. However, this induction was much weaker than its induction by heat shock, and the accumulated protein could not be detected after SA treatment. This result may suggest the post-transcriptional regulation of this heat shock gene (Chang and others 2007).

Cyclophilins (Cyp) are ubiquitous proteins with intrinsic peptidyl-prolyl *cis-trans* isomerase activity, which catalyze the rotation of X-Pro peptide bonds and facilitate the *in vivo* folding of proteins. SA treatment may also lead to Cyp mRNA accumulation in bean leaves. A significant Cyp mRNA accumulation could be detected in response to heat shock or salt stress in maize or after cold stress in bean. Two putative heat shock elements were identified in the promoter region of a maize Cyp genomic clone, whereas a metal regulatory element and a third heat shock element were localized in the $5'$ untranslated leader. These findings suggested that cyclophilin might be a stress-related protein and might also play a role in the SA-mediated signal transduction processes (Marivet and others 1995).

Dehydrins, also known as late embryogenesis abundant proteins, are the most commonly observed proteins to accumulate in plants in response not only to certain abiotic stresses such as drought, temperature stress, salinity, or wounding, but also to SA (Shen and others 2004). Another osmoprotectant, glycine-betaine, is also accumulated by plants in response to high levels of NaCl, drought, cold stress, or ABA treatment, as shown in barley (Jagendorf and Takabe 2001). Additional inducers of glycine-betaine accumulation have been detected in barley seedlings, including other inorganic salts, oxidants, and organic compounds. The same concentrations of aspirin or SA that induced glycine-betaine accumulation increased the level of lipid peroxidation. Because H_2O_2 also increased the glycine-betaine level, the glycine-betaine-inducing effect of salicylates can be explained by their ability to increase the H_2O_2 level.

Osmotin was detected in tobacco cells exposed to gradually increasing concentrations of NaCl, which led to phenotypic adaptation and increased tolerance to NaCl (Singh and others 1987). The expression of an osmotin gene isolated from a cDNA library constructed from petal protoplast cultures of *Petunia hybrida* was strongly induced in leaves that were exposed to certain pathogens, or upon wounding in the damaged leaf. Moreover, its transcript levels increased in response to octadecanoid pathway intermediates and treatment with aspirin or SA, indicating that this osmotin gene is also involved in stress signal transduction (Kim and others 2002).

Conclusions

The results obtained in the last few years strongly argue that SA could be a very promising compound for the reduction of the abiotic stress sensitivity of crops, because under certain conditions it has been found to mitigate the damaging effects of various stress factors in plants. Several methods of application (soaking the seeds prior to sowing, adding to the hydroponic solution, irrigating, or spraying with SA solution) have been shown to protect various plant species against abiotic stress factors by inducing a wide range of processes involved in stress tolerance mechanisms (Figure 1). It is clear that SA is part of an extremely

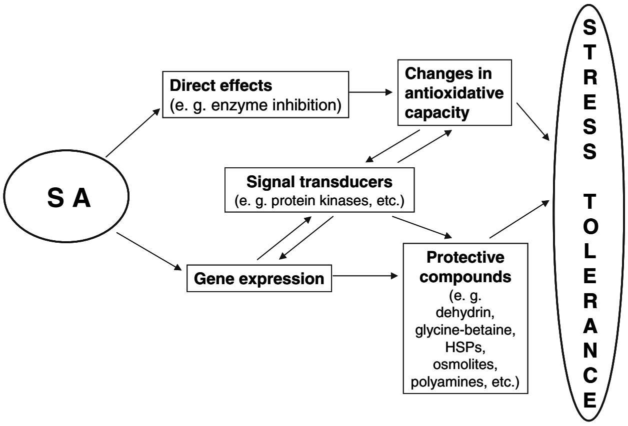

Fig. 1 Schematic model of the action of SA on the induction of abiotic stress tolerance. SA may either directly influence the activity of certain enzymes or may induce genes responsible for protective mechanisms. For more details, see text

complex signal transduction network, and its mode of action may differ in the different systems used. It may either directly influence the activity of certain enzymes, as described for catalase, or may, directly or indirectly, induce genes responsible for protective mechanisms. However, several questions remain unanswered at both the theoretical and the practical level. First, it is still not clear whether the effects of exogenous SA are direct or whether they are connected with that of endogenous SA. Furthermore, many related compounds, especially its precursors (for example, benzoic acid or o-coumaric acid), exert similar effects. This raises the question of whether SA is the only or the most important key molecule in the induction of the above-mentioned processes. In addition, several other factors such as the genetic background may also have an important influence on the action of SA. This is especially important when attempting to adapt results obtained for dicotyledonous model plants (for example, *Arabidopsis* or tobacco plants) to monocot cereals. The clarification of these questions could bring us closer to an understanding of the control mechanisms.

Acknowledgments The authors thank Barbara Harasztos for revising the English. Tibor Janda is a grantee of the János Bolyai Scholarship. This work was supported by the Hungarian National Scientific Research Foundation (OTKA T046150).

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