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# On the Role of Salicylic Acid in Plant Responses to Environmental Stresses

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## Abstract

Salicylic acid (SA) is a plant hormone more commonly known by its role in human medicine than in the field of plant physiology. However, in the last two decades, SA has been described as an important signalling molecule in plants regulating growth, development and response to a wide number of biotic and abiotic stresses. Indeed, actually, it is well known that SA is a key signalling molecule involved in systemic acquired resistance (SAR), and recent works reported a role for SA in the response to salt or drought stresses.

The precise mode of the stress hormone SA action is unclear, although it has been shown to interact in a complex manner with the antioxidative metabolism, modulating cellular redox homeostasis and leading to changes in transcription factor activities and defence gene activation. In this sense, SA activates defence signalling pathway(s) through *non-expressor of PR-protein 1* (NPR1), which is one of the few known redox-regulated proteins in plants.

Different synthetic chemicals are able to mimic the ability of SA to activate resistance to various stresses, both biotic and abiotic, in plants with agronomic interest. Among these chemicals, 2,6-dichloroisonicotinic acid (INA) and benzo-thiadiazole (BTH) are the most widely studied compounds due to its ability to induce SAR.

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In this chapter we present the role of SA and/or some of its structural analogues in the response to some biotic and abiotic challenges in relation to their effect in the antioxidative metabolism in plants.

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**Keywords**

Antioxidative metabolism • Biotic stress • Drought stress • Oxidative stress • Salicylic acid analogues • Salt stress

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## 2.1 Introduction

Salicylic acid (SA) is a phenolic plant hormone widely distributed in plants although with basal levels differing among species. It plays an important role in the regulation of multitude of physiological processes such as seed germination, vegetative growth, photosynthesis, respiration, thermogenesis, flower formation, seed production or senescence. Effect of SA on these processes can be direct or indirect, because SA is implicated also in the synthesis and/or signalling regulation of other plant hormones. Indeed hormonal relations and especially the antagonisms between SA and abscisic acid (ABA) or jasmonic acid (JA) are currently highly studied and discussed. However, SA is mainly known for its central role in plant pathogen interaction, and during the last two decades, hundreds of papers regarding its implication in the plant response to biotic stress have been published. Under biotic stress conditions, SA fulfils a key function as an endogenous signal mediating in local defence responses and SAR, as well as contributing to maintain cellular redox homeostasis through the regulation of antioxidant enzyme activity. In addition, SA is required for pathogenesis-related (*PR*) gene expression (Goellner and Conrath 2008), and increases in the amount of endogenous SA levels are correlated with expression of *PR* genes and development of SAR. In addition, exogenous SA application, as well as its functional analogues or derivatives, induces *PR* gene expression and increases resistance to diseases. In this sense, some synthetic chemicals are able to mimic the ability of SA to activate resistance to biotic and abiotic stresses in plants of agronomic interest. Among these chemicals 6-dichloroisonicotinic acid (INA) and benzothiadiazole (BTH) are the most widely studied compounds by its ability to induce SAR.

On the other hand, recently works point out an important role for SA in response to abiotic stresses such as drought, chilling or saline stress (Takatsuji and Jiang 2014). However, the role of SA in these abiotic situations is even less unravelled, and several contradictory data and antagonisms are reported. Indeed, in the bibliography we can find that the effects of exogenous SA applications on physiological parameters differ depending on the concentration applied and plant species tested. For example, the effect of SA in salt-stressed plants seems to depend on different factors, including the SA concentrations used, the plant species, how the SA treatment is applied, the physiological state of the plant during application as well as the level of salinity and the exposure time to NaCl. Unlike the response to salt stress,

the effect of SA on water stress seems to be clearer, and an evident effect of SA improving the response to drought stress has been reported by different authors.

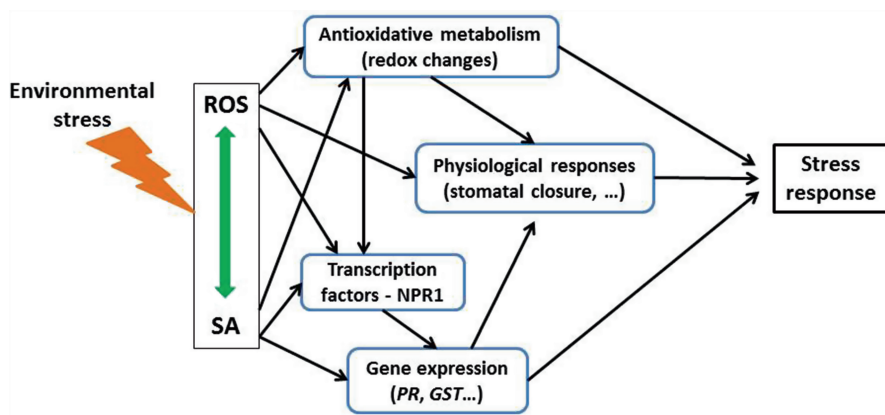
However, despite the great progress made during the last decades, the molecular and biochemical mechanisms behind these responses are not deeply well known yet. Although several binding proteins with very high affinity for SA such as tobacco SABP2 have been found, and some key components in the network of SA response such as the transcriptional factor *NPR1* have been described, the SA receptor has been not identified yet, and SA downstream signalling is not fully understood (Manohar et al. 2015). In this chapter we present the role of SA and some of its structural analogues in the response to some biotic and abiotic challenges throughout its interaction with the antioxidative metabolism in plants. In this sense, a complex interplay between SA and reactive oxygen species (ROS) in the regulation of defence genes has been also described, and several papers supported the idea that  $H_2O_2$  can be a mediator in the SA-dependent induction of *PR* genes (Garretón et al. 2002). Regarding the evidences of role of SA as regulator of plant growth and development, the reader is referred to other chapter or reviews on this subject (Rivas-SanVicente and Plasencia 2011).

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## 2.2 SA and ROS Interplay

Although most studies on signal interaction have focused on phytohormone interactions, it is largely described that ROS are used by plants as signalling molecules during development and stress situations. Activation of an ROS burst is a common response to both biotic and abiotic stresses (Miller et al. 2009). To provide an appropriate defence response to diverse stress stimuli in different physiological stages and tissues, the defence signalling must be conducted under a complex and strongly regulated network within an accurate physiological context. Different studies indicate that plants are able to coordinate signals from diverse signalling pathways and to prioritise among them and that a combination of stresses could lead to unique gene expression profiles (Xu and Brosché 2014). Moreover, ROS are also used by plants as second messengers in signal transduction cascades in a variety of processes, being their accumulation crucial for plant development as well as defence. Thus, ROS production and scavenging are intimately linked, and the balance between them together with other signalling pathways such as those mediated by SA will determine defence signalling output (Fig. 2.1).

Early in the 1990s, SA level and ROS metabolism were found to be closely connected, describing that SA increases correlated with increases in ROS production. However, recent studies point out novel antagonistic interplay between SA and ROS signalling which could explain the high degree of responsiveness of plant to different situations and biotic and abiotic challenges (Chen et al. 1993; Xu and Brosché 2014). For example, recently it has been described in several different mutants that the constitutive activation of defence by SA signalling interferes with the plant's ability to properly respond to an ROS signal from the apoplast after ozone stress. Treatment of plants with ozone generates a burst of apoplastic ROS, but in plant



**Fig. 2.1** Interplay SA-ROS in plant stress response

with high SA levels and constitutive defence activation, it is attenuated and vice versa, so the authors conclude that there could exist an attenuation of apoplastic ROS signalling by SA at the level of gene expression. Thus, these recent results strongly support the idea that a coordinated network integrating diverse signalling pathways such as those mediated by SA and ROS pathways plays a key role in environmental stress responses (Xu and Brosché 2014) (Fig. 2.1).

On the other hand, it has been also reported that there is a decrease of some antioxidant enzymes such as ascorbate peroxidase (APX) and catalase (CAT) under stress situations. In this sense, it has been shown that SA and some of its analogues inhibit the activity of CAT and APX enhancing the accumulation of  $H_2O_2$  that can perturb the cellular redox state. In contrast with CAT or APX, the guaiacol peroxidases, which participate in the cross-linking of cell wall components, are not inhibited by SA (Durner and Klessig 1996; Apel and Hirt 2004; Mittler et al. 2004; Garretón et al. 2002). More recently, biochemical screens for SA-binding proteins resulted in the identification of multiple enzymes, such as CAT, APX, the E2 subunit of  $\alpha$ -ketoglutarate dehydrogenase and glutathione S-transferases, inhibited upon binding to SA (Fu and Dong 2013). However, the inhibition of CAT by SA does not always occur, especially in abiotic stress responses. For example, SA-accumulating *Arabidopsis* lines presented higher CAT levels than wild-type line (Mateo et al. 2006).

## 2.3 SA Role in Biotic Stress and SAR

Early last century, several studies showed that when a plant was infected by a pathogen, some systemic defence mechanisms were activated involving an increased resistance against subsequent pathogen attacks. Hypersensitive response (HR) is one early response associated with necrotic lesions at the site of pathogen entry, ROS accumulation and activation of defence-related genes that (among others)

encode several families of PR proteins. After that, increased levels of PR gene expression are observed in non-inoculated tissues, and the development of SAR, as a broad resistance to different pathogens, is underway (Conrath et al. 2001; Gary and Goodman 2004; Vlot et al. 2009). Nevertheless, a systemic resistance implies the existence of a signal that can be transmitted through tissues. In this sense, an intensive research has focused in the search of the key in the activation of response's defence against pathogens and the establishment of SAR.

Although elicitors from various extracts of plants and microorganisms, or other compounds such as  $\beta$ -aminobutyric acid, have been described as activators or resistance inductors (Oostendorp et al. 2001), several early studies carried out in cucumber, *Arabidopsis* and tobacco showed that SAR induction was dependent on SA accumulation, and it was also correlated with PR gene expression (Yalpani et al. 1991; Durrant and Dong 2004). SA was described as endogenous signal in the resistance response at first time in 1979 in tobacco when White (1979) observed that acetyl salicylic acid (aspirin) induced resistance to *tobacco mosaic virus* (TMV), increasing PR protein accumulation and reducing lesion numbers. Subsequently, Malamy et al. (1990) observed that the endogenous salicylic acid levels in resistant but not susceptible cultivars increased in infected and uninfected leaves after TMV inoculation. Moreover, prior to the establishment of SAR, SA levels increase in both inoculated and non-inoculated systemic tissues (Kessmann et al. 1994; Sticher et al. 1997). In addition, different studies showed that both high endogenous levels of SA correlated with enhanced resistance to pathogen infection and transgenic plants defective for SA biosynthesis, or in which SA was removed quickly, developed a greater susceptibility to diseases and were unable to induce SAR (Bowling et al. 1994; Ryals et al. 1996). In both cases disease resistance and PR expression could be restored by treatment with exogenous SA or synthetic analogues, being this issue discussed below.

On the other hand, various studies suggested that, after a pathogen attack, changes in the concentration of SA have an effect on the maintenance of the redox state of the cell, probably by regulating the expression of genes encoding antioxidants (Rao and Davis 1999; Vanacker et al. 2000). It has been described that biotic stress situations increase the ROS production which could act as second messengers mediating SA pathways for expression of defence genes (Yoshioka et al. 2008; Torres 2010) (Fig. 2.1). In this sense, it has been also reported that high concentrations of SA can act uncoupling oxidative phosphorylation and hence the respiration chain, stimulating ROS generation in mitochondria and also inducing the alternative respiratory pathway (Moore et al. 2002). Moreover, antioxidants such as glutathione (GSH) can block the expression of PR genes induced by exogenous application of  $H_2O_2$  and other pro-oxidants (May et al. 1998). However, GSH levels increased significantly in soy cells after incubation for 2 days with SA or its analogues (Knörzer et al. 1999). In addition, it has been described that GSH could regulate the expression of SA-dependent genes via NPR1, after exposure to the pathogen (Urbanek and Müller 2006). NPR1 protein is a transcriptional factor whose location or activity was influenced by the redox state of the cell (Mou et al. 2003). In response to avirulent pathogen treatments (or other inducers of SAR), the *npr1* mutant (also

known as *nim1* or *sai1*) accumulated SA like the wild type but was unable to develop SAR and express *PR* genes. However, overexpression of the NPR1 protein leads to constitutive expression of *PR* genes in the absence of inducers, suggesting that NPR1 is a positive regulator of SAR required for the translation of the signal accumulation of SA and expression of resistance genes (Cao et al. 1994; Mou et al. 2003). In this sense, it has been suggested that the conformation of NPR1 is sensitive to cellular redox changes. In the absence of SA, NPR1 is localised in the cytoplasm as oligomer, whereas SA accumulation induces redox changes leading to the monomerization of NPR1, probably by intermolecular disulphide bond reduction, allowing it to be transported to the nucleus. Then NPR1 in the nucleus promotes the binding of transcription factors to SA-responsive promoters, regulating the expression of *PR* genes (Mou et al. 2003; Deprés et al. 2003). The inhibition of the reduction of NPR1 and therefore its monomerization lead to a decrease in the expression of *PR* genes. Diverse data indicate that SA interactions with antioxidative enzymes, such as CAT and APX, modify the redox state enough to promote NPR1 reduction to monomers and their entry into the nucleus. However, the molecular mechanisms behind SA-induced responses and its link with ROS metabolism are still not completely understood.

Other novel mechanisms by which NPR1 mediates SA responses are being currently studied, and also NPR1-independent pathways are being reported, suggesting that other yet unknown proteins could be important in SA signalling (Robert-Seilanianantz et al. 2011). For additional information about the studies that established the SA as endogenous signal in SAR, we refer the reader to reviews on this topic such as those by Vlot et al. (2009), Robert-Seilanianantz et al. (2011) and Takatsuji and Jiang (2014).

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## 2.4 SA Analogues

Systemic acquired resistance (SAR) is a highly desirable form of resistance that protects against a broad spectrum of pathogens. Thus, following the identification of SA as an essential endogenous signal for SAR, it started a period of intense search to identify synthetic chemicals able to mimic the ability of SA to activate resistance to various stresses, both biotic and abiotic, in plants with agronomic interest. During the two last decades, considerable progress have been done, and a high number of chemical signals, SA and non-SA-related, contributing to SAR, have been isolated and characterised (Walters et al. 2013). Generally, these chemical resistance inducers do not directly affect the pathogens, so they are less likely to lead to resistance in the pathogens, a problem that often arises with fungicides and bactericides. Currently, some of these chemicals are produced commercially and broadly used in agriculture as chemical defence inducers (also known as ‘plant activators’). However, this resistance induction is normally not complete, because it depends on the genotype and environment factors. In this sense, we can find early references in the literature describing differences among species. For example, in wheat *PR1* genes are induced by pathogen infection but not by SAR chemical inducers (Molina et al. 1999), while in corn both pathogenic and chemical inducers increase *PR1*

expression (Morris et al. 1998). In addition, this response could be due to direct activation of defences, or by a priming effect on cells, resulting in an 'enhanced status' defences to face the next pathogen attack (Goellner and Conrath 2008).

In any case, these chemicals act on the SA pathway in plants, inducing expression of *PR* genes and leading to partial resistance against viral, bacterial and fungal pathogens (Friedrich et al. 1996). Moreover, different works evidence that BTH and INA may activate SA signalling downstream of SA accumulation (functional analogues), while other compounds may induce SAR stimulating SA accumulation (chemical inducers). In this part, we will focus on the most studied SA functional analogue, BTH and its role related with ROS metabolism. For more information about other SAR inducers (SA or non-SA-related) and its action mechanisms, we suggest to readers the following reviews published recently (Walter et al. 2013; Aranega-Bou et al. 2014; Gao et al. 2014; Bektas and Eulgem 2015).

The first synthetic SA analogue described to induce defence was the 2,6-dichloroisonicotinic acid and its methyl ester (both referred to as INA) (Mettraux et al. 1991; Kessmann et al. 1994; Malamy et al. 1996). INA was reported to mimic several proposed biochemical and physiological effects of SA, such as inhibition of CAT and APX activity, the cellular  $H_2O_2$  accumulation and induction of *PR* gene expression (Chen et al. 1993; Conrath et al. 1995; Durner and Klessig 1996). INA has been shown as an effective resistance inducer against major fungal and bacterial pathogens in various crops under both greenhouse and field conditions. Moreover, INA was completely systemic and did not require the accumulation of SA for the activation of SAR response (Mettraux et al. 1991). Although derivatives of the INA were not marketed as agrochemicals due to its phytotoxic effect on some crops, INA is still used as an important tool to investigate the mechanisms, whereby chemical compounds induce SAR (Oostendorp et al. 2001; Bektas and Eulgem 2015).

Some years later, another synthetic chemical, benzo (1,2,3) thiadiazole (BTH) and derivatives (Kunz et al. 1997), was reported as an inducer of defence responses against a broad spectrum of diseases in various crops, especially against fungal infections, helping to reduce the penetration rate (Görlach et al. 1996; Benhamou 1996; Tally et al. 1999; Gary and Goodman 2004; Darras et al. 2006) but also against bacterial and viral infections (Friedrich et al. 1996; Lawton et al. 1996; Anfoka 2000; Hafez et al. 2004). In contrast to INA, BTH was sufficiently well tolerated by most crops. Therefore, the benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH or acibenzolar-S-methyl or ASM) was marketed as the first effective synthetic activator of SAR for practical agronomic use under the names BIONR, ACTIGARDR and BOOSTR.

BTH is the SA functional analogue better known and studied. Recent data suggested that BTH is converted into acibenzolar by SABP2 protein (Bektas and Eulgem 2015). In this work, when BTH was sprayed on SABP2-silenced tobacco plants, they failed to induce PR1 protein expression and SAR. On the other hand, when the same transgenic plants were treated with acibenzolar, SAR was fully induced (Bektas and Eulgem 2015). Nevertheless, information regarding the biochemical action mechanism of BTH remains unclear, and the protective effect depends on both crops and concentration. While some reduction in growth was reported in herbaceous plants such as cauliflower or pea plants (Godard et al. 1999;



Clemente-Moreno et al. 2010), a positive effect on the growth of peach plantlets under in vitro conditions has been described (Clemente-Moreno et al. 2012).

Similar to SA, the exogenous application of BTH leads to the expression of *PR* genes and the change in the activity of some antioxidant enzymes, triggering the accumulation of ROS by the inhibition of the two main  $\text{H}_2\text{O}_2$  scavenger enzymes, CAT and APX (Wendehenne et al. 1998). In bean plants, treatment with BTH resulted in resistance against *Uromyces appendiculatus* (rust), and parallel to this resistance, increased levels of apoplastic  $\text{H}_2\text{O}_2$  and peroxidase (POX) activity were recorded, which led to the strengthening of the cell walls (Iriti and Faoro 2003). Furthermore, treatment with BTH increased apoplastic PR proteins, as PR2 (glucanases) and PR3 (chitinase), which could contribute to the inhibition of pathogen spread (Iriti and Faoro 2003). Similar response has been described in in vitro peach explants, in which treatment with 10  $\mu\text{M}$  BTH increased endogenous levels of  $\text{H}_2\text{O}_2$  (Clemente-Moreno et al. 2012). Moreover, pretreatment with low concentrations of BTH induces expression of the enzyme phenyl ammonium lyase (PAL) in *Arabidopsis*, increasing its mRNA levels after an infection with *Pseudomonas syringae* pv tomato DC3000 (Kohler et al. 2002).

Regarding the activation of antioxidant defences, BTH treatment of soybean cells resulted in increased glutathione reductase (GR), monodehydroascorbate reductase (MDHAR) and glutathione S-transferase (GST) activities, as well as higher ascorbate and glutathione content (Knörzer et al. 1999). Liu et al. (2005) reported increases of POX, superoxide dismutase (SOD) and ascorbic acid content by BTH treatment in peach fruit. In *Plum pox virus* (PPV)-infected peach plants, BTH treatment produced an increase in GST and a reduction in dehydroascorbate reductase (DHAR) and CAT activities (Clemente-Moreno et al. 2013). Moreover, a possible BTH protection against the PPV-induced oxidative damage to the photosynthetic machinery was described (Clemente-Moreno et al. 2013). A positive effect of BTH on glutathione peroxidase (GPX), GST and GR had been also observed in pea, soybean cells and apple (Knörzer et al. 1999; Clemente-Moreno et al. 2010; Sklodowska et al. 2011). In apple, BTH treatment increased the GST and GPX activities up to 70% and 30%, respectively, but reduced APX activity and  $\alpha$ -tocopherol concentration (Sklodowska et al. 2010). However, these authors describe also an increased lipid peroxidation levels in BTH-treated plants, suggesting a possible elicitation of pro-oxidant responses by BTH (Sklodowska et al. 2010). It was demonstrated that treatment of cells with BTH produced an inhibition of the NADH: ubiquinone oxidoreductase in complex I of the mitochondrial transport chain (Van der Merwe and Dubery 2006). This enzyme is the most important in the oxidation of NADH under normal conditions, and it is also the major source of ROS generation in mitochondria (Moller 2001). This response was dependent on the concentration of BTH used and was greater than that produced by SA. However, the spectrum of protection appears to be specific for each crop. In this sense, BTH activates resistance to late blight (*Phytophthora infestans*) in tomato but not in potato (Tally et al. 1999). In pea plants, BTH treatment prior to PPV inoculation partially reduced the number of leaves showing symptoms, and in noninfected pea plants, BTH treatment increased APX, MDHAR, POX and glucose-6-phosphate dehydrogenase (G6PDH) activities (Clemente-Moreno et al. 2010).



## 2.5 Role of SA in NaCl-Stressed Plants

The role of SA in the response of plants under salinity conditions has still to be unravelled. Different authors studied the effect of exogenous SA treatments in the response to NaCl stress in different plant systems, and its effect seems to be dependent of the SA concentrations used, the plant species, the application mode of the treatment, the physiological state of the plant during the application as well as the level of salinity and the exposure time to NaCl (Table 2.1).

Some authors described that exogenous SA treatments improved plant growth under saline stress (Szepeši 2006; He and Zhu 2008; Bastam et al. 2013; Liu et al. 2014) as well as the seed germination process in the presence of NaCl (Rajjou et al. 2006; Lee et al. 2010). The pretreatment of tomato plants with low SA concentrations ( $10^{-4}$  M) improved the acclimation of tomato plants to 100 mM NaCl in hydroponic cultures. SA pretreatment improved the photosynthetic efficiency, enhanced APX and guaiacol peroxidase activity in roots and induced an accumulation of polyamines (Szepeši 2006).

The foliar SA application alleviated the NaCl-induced damage in tomato plants (He and Zhu 2008). In this work, the pretreatment was carried out by foliar spray of 1 mM SA in 10-day-old seedlings, and NaCl treatment (100 mM) was analysed at 7 and 14 days. As expected, plant growth was strongly reduced in salt-stressed plants, but this reduction was less pronounced in SA-treated plants. These authors observed a SA alleviation of the NaCl-induced oxidative stress as indicated by lower levels of lipid peroxidation and  $H_2O_2$  accumulation as well as the enhancement of the antioxidant capacity of tomato plants by increases in CAT, APX, DHAR and ASC and GSH contents (He and Zhu 2008). Moreover, it has been described that increased SA levels by pathogen infection also promote NaCl resistance. For example, root colonisation by the fungus *Piriformospora indica* triggers systemic resistance to fungal diseases and confers enhanced tolerance to salt stress in barley (Waller et al. 2005).

SA plays a role in seed germination under stress conditions, but a variability of results has been reported, and both SA-induced inhibition and promotion of seed germination have been reported. In this way, SA inhibits seed germination in a concentration-dependent manner in pea, maize, *Arabidopsis* and barley (Guan and Scandalios 1995; Borsani et al. 2001; Xie et al. 2007; Barba-Espín et al. 2011), whereas other authors showed that SA promotes germination under saline conditions by reducing the NaCl-induced oxidative damage (Rajjou et al. 2006; Lee et al. 2010).

Rajjou et al. (2006) described that SA improved the germination of the wild-type *Arabidopsis* (Ler) and the NahG transgenic line which overexpresses a bacterial salicylate hydroxylase gene that transforms SA to catechol (Delaney et al. 1995). The germination of wild-type *Arabidopsis* (Col-0) seeds was significantly delayed by NaCl, and this inhibition was even more noticeable in the presence of SA levels higher than 100  $\mu$ M, whereas lower SA concentrations, close to physiological levels (1–10  $\mu$ M), reduced the inhibitory effect of NaCl during the germination (Lee et al. 2010). These authors suggested that high SA concentrations can have a toxic effect on plant growth and development possibly due to its reported effect inducing ROS accumulation (Rao et al. 1997), whereas physiological SA levels are able to counteract the

**Table 2.1** Described effects of exogenous salicylic acid (SA) treatments in plants subjected to salt or drought stress

Stress and plant species	SA concentration	Phenotype effect	Antioxidative metabolism	References
100 mM NaCl	10 <sup>-4</sup> M	Improved acclimation	Increased APX and GPX	Szepesi (2006)
Tomato	hydroponic culture			
100 mM NaCl	1 mM SA, foliar application	Improved plant growth	Increased ascorbate, GSH, CAT, APX, DHAR	He and Zhu (2008)
Tomato				
150 mM	1–10 $\mu$ M	Germination promotion	Decreased H <sub>2</sub> O <sub>2</sub> generation	Lee et al. (2010)
<i>Arabidopsis</i>	MS agar plates			
70 mM NaCl	25–100 $\mu$ M, foliar application	Reduction of plant growth	Increased ascorbate, GSH, CAT, SOD	Barba-Espín et al. (2011)
Pea plants			Decreased APX and GR	
30–90 mM NaCl	0.5–1 mM, foliar application	Improved plant growth	Reduced electrolyte leakage, increased chlorophyll contents	Bastam et al. (2013)
Pistachio		Increased P <sub>N</sub>		
100 mM NaCl	0.1 mM, foliar application	Improved plant growth	Reduced ROS accumulation and lipid peroxidation	Liu et al. (2014)
Cotton		Increased P <sub>N</sub>	Increased CAT	
15% peg	0.5 mM, hydroponic culture	Increased sensitivity to drought	Increased electrolyte leakage and reduced photosynthesis	Németh et al. (2002)
Maize, wheat				
Drought stress	1 $\mu$ M, foliar application	Delayed symptoms	Decreased H <sub>2</sub> O <sub>2</sub> contents and lipid peroxidation	Saruhan et al. (2012)
Maize		Improved plant growth	Increased GSH, CAT, GR, MDHAR, DHAR	
Drought stress	500 $\mu$ M, soil culture	Improved plant growth	Increased SOD, CAT	Habibi (2012)
Barley		Photosynthesis protection		
		Improved WUE		
Water stress	2 mM (in watering)	Improved plant growth	Increased CAT, SOD and proline	Ying et al. (2013)
Red bayberry				
15% peg-6000	0.5 mM, hydroponic culture	Alleviate plant growth inhibition	Increased ascorbate, GSH	Kang et al. (2013)
Wheat			Gene induction ( <i>GST1</i> , <i>GST2</i> , <i>GR</i> , <i>MDHAR</i> )	

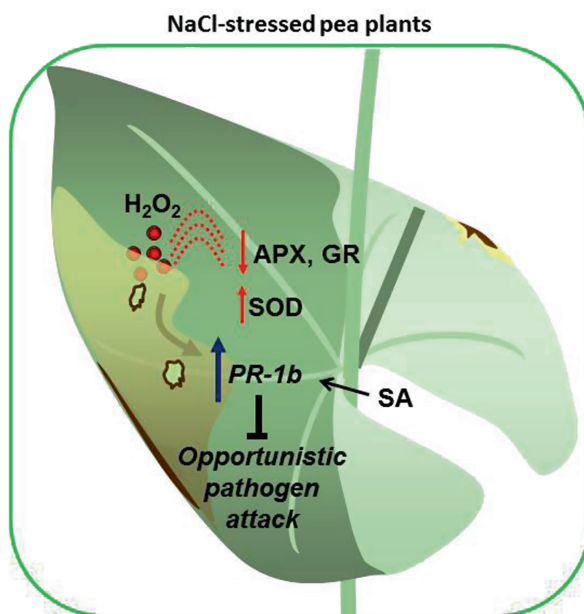
inhibitory effect of NaCl in the germination process by lowering the salt-induced H<sub>2</sub>O<sub>2</sub> accumulation in germinating seeds (Lee et al. 2010). These results contrast to those previously reported by Borsani et al. (2001) that found that SA enhanced the deleterious effect of NaCl or drought stress in *Arabidopsis* seedlings by increasing the

rate of ROS generation in photosynthetic tissues. Wild-type *Arabidopsis* (*Ler*) seeds were unable to germinate in the presence of 100 mM NaCl, whereas the SA-deficient transgenic *NahG Arabidopsis* line was able to germinate under the same conditions. According to Lee et al. (2010), the ability of the *NahG* seeds to germinate under NaCl stress can be due to the antioxidant activity of catechol.

SA could be also related to plant acclimation to saline conditions. NaCl-adapted tomato cells contained a lower concentration of SA than unadapted cells (Molina et al. 2002). The adaptation process to NaCl was also related with a higher antioxidative capacity because salt-adapted cells also contained higher basal levels of APX and GR activities (Molina et al. 2002). Barba-Espín et al. (2011) observed that SA negatively affects the response of pea plants to NaCl stress. In this work, pea seeds and seedlings were treated with different SA levels (25, 50 and 100  $\mu$ M). In the absence of NaCl, 100  $\mu$ M SA significantly reduced plant growth, being the effect more evident in roots than in shoots. SA treatment had an effect on the antioxidative machinery of pea plants. For example, in the absence of NaCl, 100  $\mu$ M SA increased APX and catalase activities, whereas in the presence of NaCl, a decrease in APX as well as increases in SOD and GST activities took place, being this response correlated with an accumulation of  $H_2O_2$  in these plants (Barba-Espín et al. 2011). Low SA levels produced the induction of the *PR-1b* gene in leaves from NaCl-stressed pea plants. These authors suggested that the induction of *PR-1b* gene could be an adaptive response in order to prevent a possible opportunistic fungal or bacterial infection in a weakness situation (Barba-Espín et al. 2011) (Fig. 2.2).

In a more recent work, Bastam et al. (2013) reported that the exogenous application of SA improved the tolerance of pistachio seedlings to NaCl stress (up to

**Fig. 2.2** Biochemical and molecular changes in NaCl-stressed pea plants treated with SA. In NaCl-stressed pea plants, SA increased  $H_2O_2$  contents and correlated with the activation of SOD ( $H_2O_2$ -generating enzyme) and the reduction in APX and GR (involved in  $H_2O_2$ -detoxification). Furthermore, SA induced the *PR-1b* gene in salt-damaged leaves, probably to prevent a possible opportunistic fungal or bacterial infection (Barba-Espín et al. 2011)



90 mM NaCl). The SA-treated plants showed lower NaCl-induced injured symptoms, a better growth rate, higher chlorophyll contents and photosynthetic capacity than the non-treated plants. In this case, authors used SA concentrations ranging from 0 to 1 mM, and the treatments were applied by foliar spray. The foliar application of 0.1 mM SA also improved the growth of cotton seedlings in the presence of 100 mM NaCl. The SA-treated plants displayed better growth and photosynthetic rates and showed low ROS accumulation ( $O_2^{\cdot-}$  and  $H_2O_2$ ) and lipid peroxidation that correlated with a significant enhancement of CAT activity (Liu et al. 2014).

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## 2.6 SA and Response to Drought Stress

The effect of SA on water stress is more homogeneous than its effect on salt stress, and some early reports showed that the SA treatment could improve the response to drought stress (Munne-Bosch and Penuelas 2003; Bechtold et al. 2010; Khokon et al. 2011; Ying et al. 2013; Miura et al. 2013) (Table 2.1). Exogenous SA application induced drought tolerance in red bayberry plants, wheat seedlings, barley plants and pea plants (Ying et al. 2013; Singh and Usha 2003; Habibi 2012; Miura et al. 2013). In general, the improved drought response induced by SA is associated with an increase or maintenance of plant growth,  $P_N$ , Rubisco activity and the antioxidative capacity (Table 2.1). SA-treated bayberry plants displayed better RWC (relative water content), photosynthetic rates as well as higher CAT and SOD activity and proline contents than non-treated plants (Ying et al. 2013). In addition, SA attenuated the drought-induced oxidative stress as recorded by a decrease in some oxidative stress parameters such as lipid peroxidation and electrolyte leakage, suggesting that SA can partially protect the membrane integrity. SA increased Rubisco and SOD activities as well as chlorophyll contents in drought-stressed wheat seedlings (Singh and Usha 2003). The improvement of SA on drought tolerance of barley plants was associated with an increase in the antioxidative defences and the maintenance of photosynthesis under water stress conditions (Habibi 2012). However, in spite of the effect of SA in gas exchange parameters, plants displayed a decrease in shoot biomass (Miura et al. 2013). Similar result was described also in pea plants treated with 100  $\mu$ M SA, with a reduction in gs without effects in  $P_N$ , therefore increasing WUE (Barba-Espín et al. 2011). Miura et al. (2013) also observed that drought stress induced the expression of *PR-1* and *PR-2*, two typical SA-inducible genes, suggesting that SA accumulation may be required for drought tolerance.

In addition, plant genotypes containing high SA contents also showed a higher degree of drought tolerance. The *Arabidopsis* genotype C24 contained a SA level near fivefold higher than control genotype and showed a higher drought tolerance but also showed biotrophic pathogen resistance and tolerance to ozone (Bechtold et al. 2010). The treatment of wheat seedlings with 0.5 mM SA alleviated the growth inhibition induced by drought. This response was linked to the increase in ASC and GSH as well as the increase in the transcription of *GST1*, *GST2*, *GR* and *MDHAR* genes (Kang et al. 2013). As SA increased the antioxidant performance and decreased lipid peroxidation levels in different plant species, it has been suggested

that SA may act as an ROS scavenger (Kang et al. 2013). SA treatment increased the ASC-GSH cycle enzymes along with SOD and CAT in two maize cultivars, showing different sensibility to water stress, after 10 days of withholding water, suggesting that ASC-GSH cycle can act to remove the  $H_2O_2$  generated during the early phase of water stress (Saruhan et al. 2012).

Although different authors reported that SA treatment improves the response in water-stressed plants, as described by different authors, also an increase in sensitivity to PEG-induced drought has been described in maize plants (Németh et al. 2002). It seems that the manner of SA application has a great influence on their effects. These authors added 0.5 mM SA in the hydroponic solutions in the presence of 15% PEG, and an increase in electrolyte leakage as well as in  $P_N$  was produced (Németh et al. 2002). These results were supported by the data observed in the transgenic *NahG Arabidopsis* line, in response to abiotic stress (Borsani et al. 2001). These authors described that the *NahG* line was better able to resist the oxidative damage generated by salt and osmotic stress than the wild-type plants.

The C24 *Arabidopsis* genotype responded to drought stress by decreasing the stomatal conductance (Bechtold et al. 2010). Similar results were observed in the SA-accumulating *Arabidopsis* mutants' *siz1*, *cpr5* and *acd6* that sowed reduced stomatal aperture and drought tolerance (Miura et al. 2013). In fact, it has been reported that SA reduced the stomatal conductance in a dose-dependent manner in different plant species, including *Vicia faba* (Mori et al. 2001), *Commelina communis* (Lee 1998) and *Arabidopsis* (Khokon et al. 2011). The SA-induced stomatal closure is dependent on ROS generation, because the application of antioxidant enzymes such as catalase and SOD suppressed the stomatal closure. In addition, the stomatal closure induced by SA was completely suppressed by the action of salicylhydroxamic acid (SHAM), a cell wall peroxidase inhibitor, but not by DPI (a NADPH oxidase inhibitor). These results suggested that SA induced stomatal closure by means of the ROS generated by cell wall peroxidases (Mori et al. 2001; Khokon et al. 2011; Miura et al. 2013). In the effect of SA mediating the stomatal closure, also extracellular-free  $Ca^{2+}$  seems to be involved because the use of  $Ca^{2+}$ -chelators, as EGTA, reduced the SA-induced stomatal closure (Khokon et al. 2011). However, the treatment of two maize cultivars with 1  $\mu$ M SA by foliar spraying reversed the drought-induced stomatal closure (Saruhan et al. 2012).

Therefore, it can be suggested that the induction of drought tolerance by exogenous SA application may have a significant practical application in agriculture, horticulture and forestry. In this sense, although we still have a long way to go to decipher the networks behind the control response to stress, the implications of SA and ROS and the antioxidative metabolism in response to stress, understanding the performance of SA regulation network could be key to provide to agriculture an appropriate improvement of plant defence responses to face to any stress conditions and coming environmental changes.

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