

Review paper

Salicylic acid: an effective growth regulator for mitigating salt toxicity in plants

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Abstract

Salinity is a harmful environmental factor threatening plant growth and productivity through ionic and oxidative stresses. These detrimental effects of salinity could be modulated by some plant growth regulators. Salicylic acid (SA) as a phenolic molecule regulates growth and development and also induces crucial defense mechanisms in plants under salinity. This growth regulator can also improve some physiological and biochemical processes of salt-stressed plants such as reducing Na^+ influx to the root cells and increasing essential nutrients uptake. Application of SA can also help plants to accumulate the toxic Na^+ in vacuoles through enhancing the activities of H^+ -pump- stressed plants. Some reports indicate that salicylic acid counteracts salt-induced water deficit by elevating plant osmolytes including soluble sugars, proline, and glycine betaine. These essential roles as well as the effect of SA in the augmentation of chlorophyll and photosynthetic activities can potentially improve plant growth and productivity under saline conditions. The possible cross-talks of salicylic acid with other growth regulators are also important for promoting salt tolerance and the performance of plants under stressful conditions.

Keywords: Antioxidants; Chlorophyll; Photosynthetic activity; Salicylic acid; Salt tolerance

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Introduction

Salt stress can restrict plant growth and development due to a reduction in water accessibility, ionic and oxidative stresses, and nutrient deficiencies (Rady *et al.* 2019; Abdoli *et al.* 2020). The main adverse effect of salinity is the ionic stress resulted from an increment of sodium (Na^+) and decrement of potassium (K^+) uptakes, which leads to a reduction in the K^+/Na^+ ratio in plant cells (Ghassemi-Golezani and Farhangi-Abriz 2018). The toxic levels of sodium can strongly trigger the generation of reactive oxygen species (ROS) including $\text{O}_2^{\cdot-}$ (superoxide radical) and H_2O_2 (hydrogen peroxide), resulting in a variation in the cellular redox metabolism. Plants may employ different enzymatic or non-

enzymatic defense mechanisms to cope with oxidative stress caused by salinity. Augmentation in scavenging potential of ROS in salt-stressed safflower plants is occurred through increasing the activities of catalase (CAT), superoxide dismutase (SOD) and peroxidase (POX), and enhancement of some non-enzymatic compounds such as phenolics, ascorbic acid, and α -tocopherol (Ghassemi-Golezani *et al.* 2021). Salinity can limit water availability to plants, which results in cell dehydration and inhibition of cell expansion and division. Increasing accumulation of osmoregulators such as soluble sugars, proline and glycine betaine in salt exposed plants may be a mechanism for preserving cell water potential at an optimum level. This stress may also result in

decreasing essential nutrients absorption, ion imbalance, and reduction in photosynthetic pigments and efficiency, leading to less growth and productivity of plants (Abdoli *et al.* 2020). Several strategies such as the application of plant growth regulators have been confirmed to induce stress tolerance in various plants species (Ghassemi-Golezani and Nikpour-Rashidabad 2017; Ghassemi-Golezani and Farhangi-Abriz 2018; Farhangi-Abriz *et al.* 2020).

Salicylic acid (SA) as a signaling molecule and plant growth regulator with phenolic nature has been shown to improve plant tolerance to major abiotic stresses, including salinity and osmotic stress (Khan *et al.* 2014; Nazar *et al.* 2015a). SA is synthesized via two distinct phenylalanine (PAL) (the most common pathway) and isochorismate (IC) pathways (Wildermuth *et al.* 2001; Mustafa *et al.* 2009; Jayakannan *et al.* 2015). The phenylalanine-derived pathway occurs in the cytoplasm. Briefly, the enzyme phenylalanine ammonia lyase helps to transform phenylalanine to trans-cinnamic acid. Trans-cinnamic acid is then converted to benzoic acid (Horváth *et al.* 2007; Mustafa *et al.* 2009). In the end, salicylic acid is produced from benzoic acid through activation of benzoic-acid-2-hydroxylase (Jayakannan *et al.* 2015). In another pathway that takes place in chloroplasts, SA is produced from chorismate through two key enzymes including isochorismate synthase (ICS) and isochorismate pyruvate lyase (IPL) (Métraux 2002; Garcion *et al.* 2008; Rekhter *et al.* 2019; Sharma *et al.* 2020). The SA can be applied either as seed pretreatments or foliar spray to induce major

abiotic stress-tolerance mechanisms (Sheteiwy *et al.* 2019; Ghassemi-Golezani and Abdoli 2021). Exogenous SA can influence plant growth and performance, depending on concentration and plant species. Several studies demonstrated that SA may promote plant functions and resistance in low concentrations. Foliar application of 1 mM SA increased the growth and defense capabilities of plants and decreased ion toxicity under saline conditions (Farhangi-Abriz and Ghassemi-Golezani 2018; Abdoli *et al.* 2020). However, inhibition of growth and induction of ROS production by a high concentration of salicylic acid has also been reported for many plant species (Chao *et al.* 2010; Miura and Tada 2014). Moreover, various molecular studies have established that SA can regulate many processes in plants, thereby enhancing their salt tolerance (Chao *et al.* 2010; Csiszar *et al.* 2014; Pirasteh-Anosheh *et al.* 2021). Thus, this review is focused on discussing the mechanisms of SA action in regulating physiological and biochemical processes in salt-subjected plants.

Nutrient uptakes

The ameliorative effects of SA on limiting Na⁺ uptake and maintaining the optimum ratio of K⁺/Na⁺ in plant cells can result from the regulation of some H⁺-pumps including H⁺-ATPase and H⁺-PPase (Ghassemi-Golezani and Abdoli 2021) which play a critical role in Na⁺/H⁺ antiporters function. The SOS1 (located in the plasma membrane) and NHX1 (located in vacuolar membranes) are two Na⁺/H⁺ antiporters involved in the exclusion of Na⁺ from the cytosol

and/or accumulation of Na⁺ in vacuoles to prevent Na⁺ toxicity. Activation or inhibition of the H⁺-ATPase in the plasma membrane can modulate membrane potential, thereby adjusting ion flux at the plasma membrane (Ward *et al.* 2009). Manipulation of genes related to these antiporters is a novel technique for retaining ionic homeostasis to cope with salinity (Yamaguchi *et al.* 2013; Keisham *et al.* 2018). Overexpression of NHX1 antiporter has been shown to enhance salt tolerance of Arabidopsis (Apse *et al.* 1999), oilseed rape (Zhang *et al.* 2001), tomato (Zhang and Blumwald 2001), mung bean (Kumar *et al.* 2017), and maize (Zörb *et al.* 2005). Vacuolar accumulation of Na⁺ is important for the maintenance of low cytosolic Na⁺ concentration and is considered as a key mechanism of plants against salt stress (Ghassemi-Golezani and Farhangi-Abriz 2018). This accumulation is achieved by transmembrane Na⁺/H⁺ antiporters. The protons are pumped by H⁺-ATPase (V-ATPase) and H⁺-pyrophosphatase (V-PPase) (Bassil and Blumwald 2014) into vacuoles and then sent out of the vacuole by Na⁺/H⁺ antiporter in exchange with Na⁺. Increased activity of H⁺-ATPase by SA has been corroborated to have remarkable effects on diminishing Na⁺ toxicity, thus regulating ionic balance, plant growth, and improving salt tolerance of soybean plants (Ghassemi-Golezani and Farhangi-Abriz 2018).

SA protects the membrane and helps to minimize the injurious effects of Na⁺ and Cl⁻ ions in salt stressed-plants (Zhu 2003; Pirasteh-Anosheh *et al.* 2017), thereby improving ion balance in plant cells. Although some reports

suggest that SA treatment reduces a few nutrients in plants (El-Tayeb 2005; Gunes *et al.* 2007; Szepesi *et al.* 2009), the most recent report revealed that SA limits Na⁺ absorption, while enhances K⁺, Ca²⁺, Mg²⁺, Fe²⁺, Mn²⁺, Zn²⁺, N and P contents in plants (Ghassemi-Golezani and Abdoli 2021). It has been found that the NPR1-dependent SA signaling is essential for salt tolerance by limiting the transmission of sodium to the upper part of the Arabidopsis plants (Jayakannan *et al.* 2015). SA pretreatment could induce H⁺-ATPase activity, which minimizes membrane depolarization and K⁺ leakage via GORK channels under salt stress (Jayakannan *et al.* 2013).

ROS generation and antioxidant capacity

The oxidative stress is measured in terms of ROS generation. The increment in ROS generation as a result of salinity is responsible for increasing lipid peroxidation and electrolyte leakage (Ismail *et al.* 2014), which can lead to cell death (Miura and Tada 2014). Redox homeostasis in plants is retained by the suitable equilibrium between ROS generation and scavenging (Apel and Hirt 2004). Exogenous application of SA induces the scavenging and antioxidant potential of plants including enzymatic (superoxide dismutase, ascorbate peroxidase, peroxidase, and polyphenol oxidase) and non-enzymatic antioxidants (ascorbic acid, carotenoids, and α -tocopherols) under salt stress (Gill and Tuteja 2010; Pirasteh-Anosheh and Emam 2018; Ghassemi-Golezani *et al.* 2021). Reduction in oxidative stress in SA-treated ajowan (*Trachyspermum ammi* L.) plants

could be ascribed to reducing Na^+ and enhancing K^+ absorptions (Abdoli *et al.* 2020). Depending on its concentration, SA might have a different effect on stressed plants by inducing antioxidant defenses at low concentrations or inducing hypersensitive responses at high levels (Pirasteh-Anosheh *et al.* 2015). Different oxidative and scavenging statuses of various plant species exposed to salinity in response to SA application are shown in Table 1.

Reactive oxygen species oxidize membrane lipids by stimulating lipoxygenase activity, which leads to gel-phase in membranes. The activity of this enzyme is inhibited by SA under salt stress (Palma *et al.* 2013). According to Csiszar *et al.* (2014), SA can induce the expression of glutathione S-transferase genes, which improves detoxification processes under salinity. Moreover, overexpression of *OsWRKY45* by salicylic acid increases endogenous SA and averts membrane damage by minimizing the H_2O_2 content in salt-stressed *Oryza sativa* (Chao *et al.* 2010). Application of 0.5 mM SA was reported to induce salt tolerance in *Triticum aestivum* due to enhancing transcription of some antioxidant genes including *GPX1*, *GPX2*, *DHAR*, *GR*, *GST1*, *GST2*, *MDHAR*, and *GS*, and increasing the activity of ascorbate glutathione pathway enzymes (Li *et al.* 2013). The ROS-mediated oxidative stress may be also alleviated by SA through increasing proline accumulation in plant tissues (Sorkheha *et al.* 2012). Moreover, it has been shown that endogenous SA increases significantly under saline conditions. Further increase in endogenous SA by exogenous application (Abdoli *et al.* 2020)

can elevate its benefits in improving salt tolerance, since SA may act directly as an antioxidant (Popova *et al.* 2009).

Enhancement of phenolic compounds and secondary metabolites by salicylic acid has been well established in various reports (Ghassemi-Golezani and Nikpour-Rashidabad 2017; Farhadi and Ghassemi-Golezani 2020), which can improve the antioxidant capacity of plants in detoxifying ROS under adverse conditions. It has been proved that SA can enhance the synthesis of phenolics, flavonoids, and anthocyanins contents as non-enzymatic antioxidants (Chaparzadeh and Hosseinzad-Behboud 2015; Abdoli *et al.* 2020; Ghassemi-Golezani *et al.* 2020a). Farhadi and Ghassemi-Golezani (2020) reported that foliar spray of SA increases the accumulation of phenolics in the *Mentha pulegium* leaves through stimulating phenylalanine ammonia lyase activity. Some investigations revealed that the essential oil as a plant secondary metabolite with antioxidant capacity can be also influenced by salicylic acid (Mirzajani *et al.* 2015; Elyasi *et al.* 2016). Seed pretreatment with SA enhanced essential oil of dill plants under salinity (Ghassemi-Golezani and Nikpour-Rashidabad 2017). This enhancement might be related to the up-regulating of enzymes involved in the secondary metabolism by SA (Sheteiwy *et al.* 2019). Essential oil with antioxidant capacity plays a key role in scavenging ROS in stressed plants by amplification of plant defense system. An increase in antioxidant activity of essential oil of *Thymus daenensis* was found as a result of SA spraying (Ghassemi Pirbalouti *et al.* 2014). The highest

Table 1. Changes in oxidative and scavenging status of salt exposed plants in response to salicylic acid

Plant species	SA treatment	Response	References
<i>Trachyspermum ammi</i> L.	Foliar treatment	Stimulating antioxidant enzymes and inhibiting H ₂ O ₂ and O ₂ ^{•-} generations	Abdoli <i>et al.</i> 2020
<i>Brassica nigra</i>	Foliar treatment	Elevating antioxidant capacity via enhancing secondary metabolites including anthocyanins, phenolics, and flavonoids contents	Ghassemi-Golezani <i>et al.</i> 2020b
<i>Brassica parachinensis</i> L.	Foliar treatment	Amelioration of detrimental impacts of salinity through stimulation of antioxidants, AsA-GSH cycle, and the glyoxalase enzymes	Kamran <i>et al.</i> 2020
<i>Mentha pulegium</i>	Foliar treatment	Enhancing catalase, ascorbate peroxidase, and superoxide dismutase activities and total phenol contents, and reducing H ₂ O ₂ and lipid peroxidation	Farhadi and Ghassemi-Golezani 2020
<i>Glycine max</i>	Foliar treatment	Reduction in ROS generation and induction of antioxidant enzymes	Farhangi-Abriz and Ghassemi-Golezani 2018
<i>Hordeum vulgare</i>	Foliar treatment	Increasing antioxidant enzymes activities	Pirasteh-Anosheh and Emam 2018
<i>Anethum graveolens</i> L.	Seed pretreatment	Enhancing in antioxidant enzymes activities and essential oil content of different organs	Ghassemi-Golezani and Nikpour-Rashidabad 2017
<i>Solanum lycopersicum</i>	Seed pretreatment	Mitigating salt stress-injury through altering the expression pattern of GSH-based H ₂ O ₂ -metabolizing enzymes such as <i>SIGSTT2</i> , <i>SIGSTT3</i> , <i>SIGSTF4</i>	Csiszár <i>et al.</i> 2014
<i>Hordeum vulgare</i>	Foliar treatment	Reduction in NaCl-accrued oxidative stress via minimizing MDA and ROS contents	Fayez and Bazaid 2014
<i>Medicago sativa</i>	Culture treatment	Induction of POX, SOD, APX, DHAR, and GR activities	Palma <i>et al.</i> 2013
<i>Vigna radiata</i>	Foliar treatment	The decline in oxidative stress	Nazar <i>et al.</i> 2011

APX: Ascorbate peroxidase; AsA-GSH: Ascorbate glutathione; CAT: Catalase; DHAR: Dehydroascorbate reductase; GR: Glutathione reductase; GSH: glutathione reductase; H₂O₂: Hydrogen peroxide; MDA: Malondialdehyde; O₂^{•-}: Superoxide radical; POX: Peroxidase; ROS: Reactive oxygen species; SA: Salicylic acid; SOD: Superoxide dismutase

antioxidant capacity of essential oils was observed in plants treated with 100–300 ppm SA under 4000 ppm NaCl, using DPPH and linoleic acid methods (El-Esawi *et al.* 2017). Moreover, SA can alter the quantity and quality of some volatile organic compounds. Exogenous application of SA caused a notable increase in trans-pinocarveol, cis-isopinocarveyl acetate, trans-carveol, and trans-pinocarveyl acetate of *Egletes viscosa* plants

(Batista *et al.* 2019). Increasing specific essential oil compositions such as α -pinene, β -pinene, camphene, cineol, and terpinolene by SA has been confirmed by El-Esawi *et al.* (2017). These changes by SA through up-regulation of terpenoid biosynthetic pathway at the transcriptional level (Tounekti *et al.* 2013) can improve the antioxidant capacity of essential oil in plants.

Osmolytes

Osmo-regulators have a critical role in maintaining cell water potential at an optimum level (Farhangi-Abriz and Ghassemi-Golezani 2018) and protecting DNA and structures of macromolecules (Juan *et al.* 2005), especially under salinity. Alvarez *et al.* (2003) reported that salt tolerance of sunflower could be promoted by increasing osmolytes including proline and decreasing ethylene synthesis. Further increment in soluble sugars, proteins, and glycine betaine by foliar spray of salicylic acid under salinity could result from activation of some enzymes involved in sugar (Shashi *et al.* 1986) or proline metabolisms (Farhadi and Ghassemi-Golezani 2020). Application of SA enhances the synthesis of soluble sugars, proline, and glycine betaine in salt subjected rapeseed plants, especially under 10 dS m⁻¹ NaCl. The strong correlation between endogenous SA and soluble sugars demonstrates that SA content is one of the main factors regulating osmo-protective mechanisms in stressed plants (Farhangi-Abriz *et al.* 2020). The augmentation of proline content by SA may be achieved via increment in pyrroline-5-carboxylate reductase and γ -glutamyl kinase, and decrement of proline oxidase activities (Nazar *et al.* 2015b; Farhadi and Ghassemi-Golezani 2020). It has been also shown that SA application may cause a decline in proline content via enhancing chlorophyll synthesis since both are synthesized from the glutamate as a precursor (Abdoli *et al.* 2020). Salicylic acid may stimulate biosynthesis of the precursor betaine aldehyde, leading to an increment in glycine betaine content (Singh and

Gautam 2013). These elevations in osmolytes contents could result in higher leaf water content (Abdoli *et al.* 2020). Increasing root growth by SA can also expand the area of water and nutrient absorption, thereby improving the water and osmolytes status of plants under saline conditions. It is also revealed that a high root/shoot ratio in SA treated plants under salinity is a mechanism that can help water and nutrient uptakes (Yamaguchi and Sharp 2010).

Photosynthetic activity

Salt stress negatively affects the photosynthetic machinery and its efficiency through influencing pigments, stomata functioning and gas exchange, thylakoid membrane structure, electron transport, and maximum quantum yield of photosystem II (F_v/F_m) (Wu *et al.* 2010; Khoshbakht and Asgharei 2015; Ghassemi-Golezani *et al.* 2020b). Increased activity of chlorophyllase and instability of protein complexes by salt stress (Chaparzadeh and Hosseinzad-Behboud 2015) may result in decreasing chlorophyll content of stressed plants (Ghassemi-Golezani *et al.* 2020a). SA can maintain chlorophyll content at a high level by either inhibiting its degradation or increasing its biosynthesis from glutamate. The increment of chlorophylls a and b, a/b ratio and carotenoids by application of SA (Fathi *et al.* 2019) is associated with the inhibiting effects of SA on Na⁺ uptake and ROS generation and increasing essential nutrients absorptions particularly magnesium, and protection against oxidative stress caused by salinity (Abdoli *et al.* 2020). A strong correlation between magnesium content and chlorophyll has

been confirmed by Farhangi-Abriz *et al.* (2020). In addition, increasing carotenoids as antioxidants by SA treatment could enhance the scavenging capacity of salt-stressed plants that reduces detrimental effects of free radicals (Abdoli *et al.* 2020; Farhadi and Ghassemi-Golezani 2020; Figure 1). According to Nazar *et al.* (2011), higher allocation of N and S to the leaves of SA-treated plants via increasing the activity of nitrate reductase and ATP-sulfurylase, increased photosynthesis in mung bean cultivars. Application of SA can also alleviate the salt-induced decrement of photosynthesis efficiency mainly through stimulating the enzyme activity of the ascorbate-glutathione pathway and enhancing glutathione (GSH) synthesis (Nazar *et al.* 2015a). The SA enhances glycine betaine production and prevents ethylene synthesis in mung bean plants, which improves photosynthesis (Khan *et al.* 2014).

The efficiency of leaf photosynthesis is correlated with F_v/F_m ratio. A decrement in this ratio is an indication of photo-inhibition that disrupts photon flux density when plants are exposed to environmental stresses. These harmful impacts of salt stress on photosynthetic efficiency could be largely eliminated by the exogenous application of SA. The F_v/F_m ratio, stomatal conductance, and net photosynthetic rate are significantly higher in leaves of SA-treated plants, resulting in better functioning of the photosynthetic machinery under saline conditions. Application of salicylic acid noticeably decreases the time needed to reach maximum fluorescence (T_{fm}) and initial fluorescence (F_0) but increases the

variable fluorescence, the performance index, and efficiency of the water-splitting complex through elevating water content and energy required for closing the reaction centers and redox state of primary quinone in the time span from initial to maximum fluorescence, resulting in an improvement of plant photosynthetic function. SA also increases the quinone pool size of safflower leaves and enhances the electron fluidity to the photosystem II reaction centers (Ghassemi-Golezani *et al.* 2020b). The SA treatment may also enhance photosynthetic activity via improving leaf number and area (Khoshbakht and Asgharei 2015). This effect of SA on leaf area is achieved by maintaining indole acetic acid and cytokinin at high levels in salt-stressed plants (Shakirova *et al.* 2003).

Plant growth and productivity

The application of SA has been confirmed to improve the growth and salt tolerance of plants. The beneficial effects of SA treatment on plant growth are related to increasing nutrients absorptions, endogenous SA, chlorophylls, and carotenoids content, and decreasing sodium toxicity and ROS generation. Enhancing phosphorus and calcium contents in plant tissues and biosynthesis of soluble carbohydrates by SA resulted in an increment in the growth of salt subjected rapeseed plants (Farhangi-Abriz *et al.* 2020). A significant positive correlation has been reported among K^+/Na^+ ratio, endogenous SA content, membrane stability index, leaf water content, chlorophyll content, antioxidant enzymes activities, root and shoot growth, and productivity

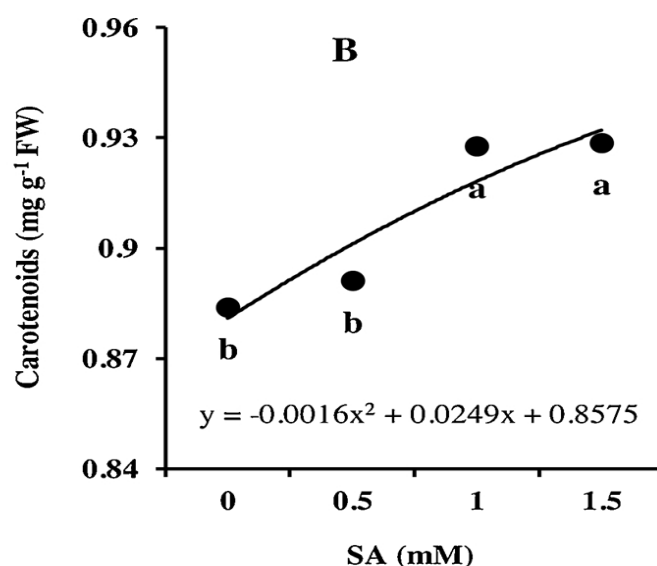


Figure 1. Effects of salicylic acid (SA) on carotenoids content of *Mentha pulegium* leaves (Farhadi and Ghassemi-Golezani 2020).

of SA treated ajowan plants under salt stress. The high root/shoot ratio of SA-treated plants is an essential way for enhancing water and nutrients availabilities to the plants under salinity (Abdoli *et al.* 2020).

Cross-talks of SA with other growth regulators

The antagonistic and synergistic interactions between plant growth regulators participate in defense signaling pathways in plants. Salicylic acid contributes to different plant developmental processes via crosstalk with other hormones such as auxins, gibberellins, abscisic acid, cytokinins, ethylene, and polyamines (Yasuda *et al.* 2008; Alonso-Ramirez *et al.* 2009; Palma *et al.* 2013; Khan *et al.* 2014; Szalai *et al.* 2016).

Auxins play an important role in many plant metabolic processes, root differentiation (Agtuca *et al.* 2014) as well as salt stress tolerance (Fahad

et al. 2015). They also promote root and shoot growth of plants under salinity and alleviates salt-induced dormancy in wheat seeds (Egamberdieva 2009). The SA and auxins act in defense mechanisms and regulate the growth of *Arabidopsis* plants. Expression of *Wes1-D* gene in *Arabidopsis thaliana* has been reported to induce salt tolerance via SA-auxin signaling (Park *et al.* 2007). Overexpression of the *PR1* gene by SA treatment in auxin *tir1 afb2* mutants shows the SA-induced auxin signaling in salt subjected plants (Iglesias *et al.* 2011). The GA signaling causes plants to adapt the adverse environmental conditions, which is mediated by SA. Salicylic acid and gibberellins (GAs) together regulate plant responses to defend against environmental stresses (Miura *et al.* 2013; Fayez and Bazaid 2014). Overexpression of GA-responsive genes is involved in enhancing SA-biosynthetic genes *ics1*

and *npr1* and endogenous SA (Alonso-Ramirez *et al.* 2009). It has been also reported that SA may upregulate the *GA3ox1* gene (GA biosynthetic gene) and causes DELLA protein degradation (Ding *et al.* 2016).

The SA may positively or negatively interact with ABA. It is antagonistic to ABA in developing systemic acquired resistance (SAR). Exogenous ABA inhibits the induction of SAR, however, activation of SAR by SA represses ABA signaling (Yasuda *et al.* 2008). High endogenous SA in ABA-sensitive mutants (*aba3* and *siz1*) improves resistance to salinity (Asensi-Fabado and Munné-Bosch 2011; Miura *et al.* 2011), which indicates that suppression of ABA signaling via SA is essential for salt tolerance. Moreover, SA may lead to the accumulation of abscisic acid (ABA), which contributes to the pre-adaptation of seedlings to salt stress by inducing the synthesis of a variety of anti-stress proteins (Shakirova *et al.* 2003). According to Szepesi *et al.* (2009), SA can trigger the accumulation of ABA in salt-stressed *Solanum lycopersicum* plants, thereby improving the osmotic adjustment, photosynthetic pigments, and growth. The control of stomatal functioning under stress conditions may be associated with changes in ABA content. Rai *et al.* (1986) have found that SA reverses ABA-controlled stomatal closure. Various environmental stresses may cause changes in the activation of the cytokinin (CK) pathway, resulting in different responses. Decreasing CK and increasing ABA have been proved in salt-subjected wheat plants. Augmentation of chlorophyll content in SA-treated plants may be

related to the regulation of cytokinin synthesis by SA, which increases endogenous cytokinin (Shakirova *et al.* 2003).

Application of SA reacts antagonistically with ethylene synthesis via inhibiting ACC activity and ethylene formation, thereby mitigating some negative impacts of salinity on plants. Khan *et al.* (2014) found that prevention of 1-aminocyclopropane-1-carboxylic acid (ACC) synthesis in SA-treated *Vigna radiata* plants under salinity leads to repression of ethylene development, which improves photosynthesis and plant growth. Oxidative stress-accrued by ethylene can be alleviated by the application of SA in plants (Tirani *et al.* 2013). Salinity-induced increment of endogenous polyamines (PAs) has also been established in several plant species (Das *et al.* 1995; Chattopadhyay *et al.* 2002). The PAs accumulation protects plants from salt injuries by removing free radicals, stabilizing cellular membrane and structures, and maintaining ion balance (Bouchereau *et al.* 1999). Increasing PAs including putrescine, spermidine, and spermine in roots of SA pretreated plants resulted in boosting stress tolerance (Szalai *et al.* 2016). The possible crosstalk of salicylic acid with other phytohormones for induction of SOS genes under salt stress is not clear and requires further investigation.

Conclusion and Future Prospects

Ionic, osmotic, and oxidative stresses due to salinity cause serious damages to plant nutritional and water status, photosynthetic activities, and plant growth and productivity. However, the

application of salicylic acid boosts the salt tolerance of plants through physiological and biochemical changes. The superior effects of SA in ameliorating salt-induced damages are largely associated with limiting Na⁺ uptake and reactive oxygen species generation by stimulating H⁺-pumps activities and augmenting enzymatic and non-enzymatic antioxidants. Increasing essential nutrients absorptions by SA treatment leads to an improvement in osmolytes accumulation and photosynthetic pigments and efficiency, thereby promoting growth and productivity of salt-

stressed plants. The possible crosstalk of salicylic with other plant growth regulators may enhance the beneficial effects of SA in mitigating sodium toxicity and improving salt tolerance. Future works may reveal other critical mechanisms of SA in alleviating biotic and abiotic stress injuries on various plants and environmental conditions.

Conflict of Interest

The authors declare that they have no conflict of interest with any people or organization concerning the subject of the manuscript.

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سالیسیلیک اسید: یک تنظیم کننده رشد مؤثر برای کاهش سمیت نمک در گیاهان

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چکیده

شوری یک عامل محیطی مضر است که از طریق تنش‌های یونی و اکسیداتیو رشد و تولید گیاه را تهدید می‌کند. این اثرات زیان‌بار شوری می‌تواند توسط برخی تنظیم کننده‌های رشد گیاهی تعدیل گردد. سالیسیلیک اسید (SA) به عنوان یک مولکول فنلی رشد و نمو را تنظیم کرده و مکانیسم‌های دفاعی حیاتی گیاهان را تحت تنش شوری القا می‌کند. این تنظیم کننده رشد می‌تواند برخی فرایندهای فیزیولوژیکی و بیوشیمیایی گیاهان تحت تنش شوری مانند کاهش ورود سدیم به سلول‌های ریشه و افزایش جذب عناصر غذایی ضروری را بهبود بخشد. کاربرد SA همچنین می‌تواند از طریق افزایش فعالیت پمپ‌های پروتونی به ذخیره سدیم سمی در واکوئل گیاهان کمک کند. این هورمون گیاهی ظرفیت آنتی‌اکسیدانی (آنزیمی و غیر آنزیمی) گیاهان تحت تنش شوری را به طور قابل توجهی افزایش می‌دهد. برخی گزارش‌ها نمایانگر آن است که سالیسیلیک اسید از طریق افزایش محتوای اسمولیت‌ها از جمله قندهای محلول، پرولین و گلیسین بتائین با کمبود آب ناشی از شوری مقابله می‌کند. این نقش‌های اساسی و همچنین اثرات SA در افزایش کلروفیل و فعالیت‌های فتوسنتزی می‌تواند قابلیت رشد و تولید گیاهان را تحت تنش شوری بهبود دهد. روابط احتمالی سالیسیلیک اسید با سایر تنظیم کننده‌های رشد هم در بهبود تحمل شوری و عملکرد گیاهان در شرایط تنش‌زا اهمیت دارند.

واژه‌های کلیدی: آنتی‌اکسیدان؛ تحمل شوری؛ سالیسیلیک اسید؛ فعالیت فتوسنتزی؛ کلروفیل