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REVIEW

Salicylic Acid and Salt Stress Tolerance in Plants: A Review

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Soil salinity has become a hot debate and has gained a great scientific interest towards global food security for an increasing population. Because salinity has numerous negative effects on crop physiology and results loss of productivity. Various attempts to overcome salinity have led to detrimental effects. However, scientists have been recruited to use certain eco-friendly techniques to increase stress tolerance in plants by rising the emission rate. One of them, which is naturally present in certain plant species, is Salicylic acid, a well-known growth regulator. Since plant hormones can monitor plant development and growth, they also serve as a strong protector against various abiotic stresses. But their concentration decreases beyond the level of protection when exposed to abiotic stressors such as NaCl stress. Thus, by increasing the amount of endogenous SA, externally supplied SA has found considerable beneficial effects on plant stress resistance. SA introduces many physiological, biochemical, and molecular modifications to plants under salt stress that include immunity. Evidence of external application of SA under salt stress tolerance in plants is discussed in this review. In addition, low SA concentrations have also been addressed and its cross-talk with other regulators.

Key words: Salicylic acid, Salt stress, Antioxidants, Hormonal cross-talk

The adverse impact on agricultural production, lead by environmental stress such as salinity has developed considerable scientific attention. The research community has made several attempts to counteract the harmful symptoms of abiotic stress in crop physiology. Plants' adaptability and protection are hindered by abiotic stresses such as drought and salt stress, which induce physiological and cellular changes. Salt stress is a common and devastating abiotic stressor that affects plant growth success, limiting crop production around the world (Munns and Tester, 2008; Mimouni *et al.*, 2016; Qiu *et al.*, 2017; Debnath *et al.*, 2018). Currently, about 20% of the world's cultivated land is affected by salt, with 2 million ha (roughly 1%) estimated to be deteriorating each year due to salinity (Qiu *et al.*, 2017; Ke *et al.*, 2018; El-Ramady 11*et al.*, 2019). FAO reported that 19% of the world's land suffered from salinity in excess of 6% (FAO and ITPS, 2015). Salinity is projected to trigger losses of over 50 percent of agriculture by 2050. The human population is growing exponentially and requires a significant rise in worldwide agricultural production. Productivity must be improved by 70 percent with an additional 2.3 billion individuals by 2050 to fulfill the burden of feeding the target population (Tilman *et al.*, 2011). Therefore, efforts to improve salt resistance in crops are crucial to ensure targeted food protection globally.

The immediate result of NaCl stress is osmotic stress due to the presence of ions surrounding the roots, preventing the extraction of water by the roots and reducing the growth of the plant. However, secondary damage (lead by ion toxicity) can also occur as a result of redox state changes and oxidative burst by ROS species production (Mittal *et al.*, 2012; Mostofa *et al.*, 2015; Nahar *et al.*, 2016). ROS accumulation is commonly cited as a key eventual outcome of aerobic metabolism (Sharma *et al.*, 2012). Excessive generation after its detoxification capability, however, exposes the plant to oxidative stress, an extremely dangerous physiological disorder that can potentially contribute to lipid peroxidation, protein oxidation, nucleic acid damage, main metabolic enzymes inhibition, and programmed cell death (Sharma and Dubey, 2005; Kamanga *et al.*, 2018).

A variety of plant physiological activities such as osmotic stress, ion disruption, nutritional disturbances, membrane damage, cell division and expansion reduction, and genotoxicity were disrupted by high salinity (Abogadallah, 2010; Safdar *et al.*, 2019). Together, these results minimize the growth of plants, and consequently the yield. However, plants use an inborn defensive mechanism to combat ion toxicity, such as the aggregation or exclusion of inorganic ions, the control of the absorption of ions by the roots and their transport through the leaves, the activation of antioxidant defense mechanisms linked to ROS, the accumulation of osmolytes and the modification of the biological membrane structure (Pirasteh-Anosheh *et al.*, 2016). This effectiveness persists up to a definite degree above which plants felt and ultimately died of water shortage (secondary drought). In addition, upsurged salinity level is thought to typically cause decreased synthesis and degradation of plant growth regulators (PGRs) in most cases (Hayat and others 2010). This contributes to total growth decline and in some cases, plant death also.

For instance, exogenous applied SA that can enhance stress tolerance in plants under saline stress maybe some of these strategies. Numerous experiments have shown that SA has added altered concentrations of sodium and potassium to various plant species and increased grain yields. For example, maize (Gunes and others 2005), tomato (Szepesi 2006; He and Zhu 2008), wheat (Kaydan and others 2007), and barley (Pirasteh-Anosheh and others 2015; Pakar and others 2016), respectively. When used at low doses, Arif, *et al.*, (2020) proposed in their literature (review) that SA may serve as a potent phytohormone that regulates several physiological and other aspects in plants.

Phytohormones are naturally occurring organic compounds that have a profound impact on plant physiological processes at low doses. Phyto-regulators play a significant role in fostering plant growth, both under normal conditions and under stress as well. Several experiments have shown that each plant hormone does not play a single biological function in plants, but plays a complex and successful role at various levels, in different tissues or under different environmental conditions (Ku, *et al.*, 2018; Yang *et al.*, 2019; Cortleven *et al.*, 2019). In this review, summarised and illustrated the multifunctional role of salicylic acid in crops during salt stress have been discussed.

SA (a novel growth regulator) improves resistance to NaCl stress:

Salicylic acid (SA) is a phenolic compound derived from plants that serve as a growth regulator as well as a primary defense mechanism. It was discovered and isolated in 1839 by German scientists in the herb meadowsweet (Filipendula ulmaria), formerly known as Spiraea ulmaria. It is found naturally in white willow (Salix alba L.). As it can be isolated from nature, it is considered a valuable "natural product". In 1828, a small amount of salicin, which is a glucoside of salicyl alcohol, was isolated by the German scientist Johann Andreas Buchner. Salicin is one of the salicylates found not only in willow tree bark but in 36 other plants as well (Raskin, 1992; Hayat *et al.*, 2010). Synthetic SA also began its first commercial production in Germany in 1874.

In addition, SA plants are primarily found in the powdered crystalline form, melt at temperatures ranging from 157 to 159 °C and have a pH equal to 2.4. It may be expressed in all ways, whether glycosylated, methylated, or both. Salicylic acid (SA; o-hydroxybenzoic acid) has received broad interest from plant physiologists among the 21 molecules of signaling. Therefore, through its comprehensive signaling cross-talk with other growth hormones, SA has the capacity to control various aspects of plant life, especially in plant defense mechanisms, to different stresses (Horva'th *et al.*, 2007; Asensi-Fabado and Munne'-Bosch 2011; Pokotylo *et al.*, 2019).

SA is a cheap and environmentally sustainable plant growth regulator, in addition to its essential physiological functionality. Therefore, its use in boosting crop yield could be exploited under natural and stressful conditions. Other compounds known as secondary metabolites such as Jasmonic Acid (JA), Brassinosteroids (BRs), and Salicylic Acid (SA) also serve as growth regulators, in comparison to main growth regulators such as auxins (AUXs), cytokinins (CKs), gibberellins (GAs), ethylene (ET) and abscisic acid (ABA), in addition to their primary protective function throughout plant pathogen infection (Figure 1). This secondary metabolite may be able to shield plants from biotic and abiotic stresses by activating a number of signaling pathways. Furthermore, SA has been shown to reduce the toxic effects of ROS created by salt stress by boosting antioxidant system activity (Belkadhi *et al.*, 2014; Mimouni *et al.*, 2016; Ma *et al.*, 2017). SA is involved in the control of many physiological processes, including increased metabolism of nitrogen, defense compound enzymes, and osmolytes inducing glycine betaine and proline in several different species (Khan *et al.*, 2010). In addition, the enhanced photosynthetic rate added by SA is correlated with increased activity of rubisco (Lee *et al.*, 2014) and absorption of K+ ion (s) (Fayez and Bazaid, 2014). Salicylic acid also greatly enhances soybean plant biomass under saline conditions (Farhangi-Abriz and Ghassemi-Golezani, 2018).

SA biosynthesis pathway

SA is synthesized along two distinct paths: the pathway of ammonia-lyase phenylalanine and the pathway of isochorism. The two processes take place in the cell at various sites, the first in the cytoplasm, while the second takes place in the cell's chloroplast. In the phenylalanine pathway, SA is synthesized from phenylalanine after a series of reactions. The enzyme called phenylalanine ammonia-lyase (PAL) plays a crucial role in the synthesis of secondary compounds such as salicylic acid, phenolic acid, and lignin along the phenylpropanoid pathway (Sorahinobar *et al.*, 2016). In the beginning, trans-cinnamic acid is produced from phenylalanine by the action of the enzyme phenylalanine ammonia-lyase (PAL). Trans-cinnamic acid is then converted to benzoic acid. The final step, the conversion of benzoic acid to SA is catalyzed by the enzyme known as 2benzoic-acid-2-hydroxylase (BA2H) (Horva'th *et al.*, 2007; Mustafa *et al.*, 2009).

As an intermediate product, SA is derived from chorismate via isochorismate in the Isochorismate pathway. Enzymes-isochorismate synthase (ICS) and isochorismate pyruvate lyase (IPL) are involved in this two-step process (Verberne *et al.*, 2000; Strawn *et al.*, 2007). The pathway of shikimic acid serves as a bridge between the digestion of carbohydrates and the biosynthesis of essential aromatic compounds such as tyrosine, phenylalanine, and tryptophan. In young pea plants, a similar result of the shikimate pathway in SA biosynthesis has been demonstrated (Szalai *et al.* 2011).

SA Pathway of signalling and transport

The transcriptional and posttranscriptional levels of the SA biosynthesis pathway are both regulated. MYBs (MY ELO BLAST; MYB 96 and MYB30), WRKYs (WRKY28 and WRKY46) and WIPK (Wound-Induced Transcription Factors of Mitogen-Activated Protein Kinase) genes have been identified in plants at the transcriptional level. These genes positively regulate the isochorismate synthase pathway of ICS gene encoding, thus increasing SA production in plants (Vidhyasekaran, 2015). RNA binding proteins (RBP) have been reported to engage in several post-transcriptional processes at the post-transcriptional level. In specific, an RBP from A. Thaliana, AtRBP-defense-related (AtRBP-DR1) has been found to influence SA biosynthesis through ICS1. For a variety of reasons, AtRBP-DR1 mutant plants accumulated fewer SA and had higher SA overexpression lines than wild-type plants, and SID2 mRNA levels were higher overexpressor lines in AtRBP-DR1 mutant plants (Qi *et al.*, 2010). After biosynthesis, SA can be freely transferred into cells, tissues, and organs (Kawano *et al.* 2004). A radio-tracer study of tobacco cell suspension culture revealed de novo activation of free SA secretion via the plasma membrane.

ROS and $Ca^{2+¿¿}$-dependent (200 μM SA), and $Ca^{2+¿¿}$-independent (20μM SA) transporters have regulated this secretion (Chen, 1999; Chen, *et al.*, 2001). In soybeans, tonoplast ABC transporter-like protein-mediated SAG transfer into the vacuole (Dean and Mills 2004), whereas tonoplast antiporter was active in tobacco suspension culture cells (Dean, *et al.*, 2005). While salicylic acid is not the mobile signal itself, SAR in other areas of the plant is still found to be formed. Furthermore, recent research suggests that the methyl ester, methyl salicylate, functions as a volatile SAR causing signal that is distributed to distant areas of the plant, including neighbouring plants (Shulaev, *et al.*, 1997; Vlot, *et al.*, 2008).

At low SA concentrations in plants, the enzyme salicylic acid carboxyl methyltransferase (16 μM) transforms SA to methyl salicylate (MeSA) (Dempsey *et al.*, 2011). Among the different forms of SA, only the methylated form (MeSA) has been shown to migrate nearby and systemically in plant tissue after pathogen infections (Seskar *et al.*, 1998). MeSA was therefore considered to be the long-distance signalling molecule through phloem translocation which moves from affected to unaffected leaves.

Physiological processes governed by SA under salinity stress

Seed germination

The seed germination regulation depends upon environmental factors and interactions between the plant hormones. The function of SA used in seed germination, other than naturally occurring phytohormones, has been controversial, as reports indicate that it can either impede germination or increase seed vigor. Furthermore, the role of SA in seed germination is affected by the genotype of the plant, the stress applied, and the experimental conditions (Lee and Park, 2010). Germination of Arabidopsis sid2 mutants missing ICS1-mediated SA biosynthesis was hypersensitive to salt stress (Lee *et al.* 2010). When the expression level of ICS1 was raised, the salt-induced germination inhibition was reversed (AlonsoRamirez, *et al.*, 2009).

The findings indicate that SA synthesis and accumulation are critical for seed germination, especially when salt stress is present. Interestingly, increased seed germination and seedling establishment in Arabidopsis under various abiotic stress conditions was noted when low 4 doses of SA were added (Rajjou *et al.*, 2006; Alonso-Ramı'rez *et al.*, 2009). Under salt stress (100-150 mM NaCl) alone, 50 percent of seed germination was found in Arabidopsis, where 80 percent was reported in the presence of SA (0.05-0.5 mM) seed germination rate.

Interestingly, SA suggested regulation of ROS balance as a mechanism by which SA modulates germination during salt tension stress (Lee *et al.* 2010). Since SA and H2O2 form a "self-amplifying feedback loop" in response to numerous stresses (reviewed by Maheswari Jayakannan *et al.*, 2015). Furthermore, H2O2 causes the aggregation of SA, and SA increases the concentration of H2O2 (Shirasu *et al.* 1997; Harfouche *et al.* 2008). Hence, under salinity conditions, the germination promotion effect of SA is to minimize oxidative damage. In addition, the proteomic analysis showed that SA induces two superoxide dismutases in Arabidopsis germinating seeds, which could lead to increased antioxidant ability (Rajjou *et al.*, 2006). SA (0.5mM for 24 h) treatment often causes a major up-regulation of protein transcription factors. Increasing seed germination by facilitating the synthesis of proteins required for seed germination as well as the mobilization or degradation of seed proteins acquired during seed maturation.

Exotic applications of three different levels of SA (0.25, 0.5, and 1mM) increased germination in Vicia faba under salinity stress (Anaya *et al.*, 2018). Salicylic acid treatment improved the germination rate of Coronilla varia seeds when they were exposed to drought stress by rising osmotic pressure (Ma *et al.*, 2017). The germination rate, percentage, and seed development of Dracocephalum moldavica seeds increase when they are primed with SA (ShaikhAbol-hasani *et al.*, 2019). SA applied exogenously to wheat increased germination indices (Fardus *et al.*, 2018). SA increased the germination parameters of coneflower plants (Darvizheh *et al.*, 2018). In soybeans, the application of SA resulted in the highest germination percentage (Aalam *et al.*, 2019).

Externally applied SA impact on growth and development

The effect of added SA varies depending on the plant species, growth level, and SA concentrations studied. The two findings of SA applied to plant physiological processes under optimal environmental conditions are observed in the contested studies. Several studies have documented that in different plant species, SA positively affects germination and/or development. For example, when the grains were subjected to pre-sowing seed-soaking treatment in SAA, improved 4germination and seedling growth were reported in wheat (Shakirova, 2007). Likewise, SA's aqueous solutions applied as a spray to soybean shoots significantly increased the growth of shoots, and especially roots also.

The 2nd characterization of Arabidopsis mutants with altered SA accumulation presented clear proof that SA was involved in plant development. cpr1/5/6 (constitutive expresser of PR1/5/6), acd1/5/6/11 (accelerated cell death1/5/6/11), dnd1/2 (defence no death1/2), isd1 (lesions simulating disease1), nudt7 (nudix hydrolase7), agd2 (aberrant growth and death), and snc1 (suppressor of nudix hydrolase7) had higher biomass than wild type (reviewed in Miura *et al.* 2011; Rivas-San Vicente and Plasencia 2011). The negatively regulated cell division and cell enlargement by SA have been proposed as a cause for the above growth variations (Xia *et al.* 2009; Hao *et al.* 2012). Similarly, 10nM, 100 µM-10mM SA treated soybean plants display increased shoot and root development, 20 percent and 45 percent, respectively, 7d after application. Shakirova *et al.*, (2003), noted that larger ears are produced by wheat seedlings treated with 50µM SA; increased cell division within the apical meristem of seedling roots.

Tomato seed pre-treatment with SA (150 ppm) improved root and shoot development under salinity tension (Ghoohestani *et al.*, 2012). Under salt tension, exogenous 4treatment of SA analogues like 2,6-dichloro-isonicotinic acid improved growth and production (Khan *et al.*, 2014). Under salt tension, foliar sprayed SA improved fenugreek plant growth, metabolism, and productivity (Babar *et al.*, 2014). Exogenous SA aids in the induction of plant growth and production, as well as the protection of plant membranes under heavy metal stress (Wang *et al.*, 2013; Yusuf *et al.*, 2013). SA (100–300 ppm) increased plant growth, specifically branching and biomass in Rosmarinus officinalis, according to El-Esawi *et al.*, (2017).

Effect on the rate of photosynthesis

Externally applied photosynthesis induced by SA is based on concentration and plant species (Ashraf *et al.*, 2010). In general, SA increased the growth rate at low concentrations (less than 100 µM) and decreased growth at moderately high concentrations (>1 mM) in different plant species (Rivas-San Vicente and Plasencia 2011). Furthermore, low concentrations of SA (less than 10 M) increased salt-induced photosynthesis in many plant species by increasing carbon fixation, transpiration, stomatal conductance, and antioxidant activity (Stevens *et al.*, 2006; Szepesi *et al.*, 2008; Nazar *et al.*, 2011; Poo'r *et al.*, 2011a). According to Lotfi *et al.*, (2020), SA at (1.5mM) had a lower impact on improving photosynthetic rate than at the optimum stage of SA (1.0 mM).

Data from several studies indicates that SA is an essential photosynthesis regulator because it affects the structure of leaves and chloroplasts (Uzunova and Popova, 2000), the closure of stomata (Melotto *et al.*, 2006), the content of chlorophyll and carotenoids (Chandra and Bhatt, 1998; Fariduddin *et al.*, 2003) and the activity of enzymes such as RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) and carbon carboxylase/oxygenase (Pancheva and Popova, 1998; Slaymaker *et al.*, 2002). Tahjib-Ul-Arif *et al.*, (2018) observed SA elevated photosynthetic rate in maize by facilitating carboxylation rate, chlorophyll amount (SPAD values), and increasing turgor. When SA doses were augmented to increase the chlorophyll content in mustard, lemongrass, and mung bean plants under stress conditions, similar findings were observed (Idrees *et al.*, 2010; Zaid *et al.*, 2019; Lotfi *et al.*, 2020).

In Satsuma mandarin leaves, exogenous SA prevents the photosynthetic apparatus from photo damage caused by intense light. This defensive effect was related to several protective mechanisms. For example, exogenous SA increased the electron transport rate and quantum yield of PSII, as well as the relative contents of D1 protein and Deg1 protease, both of which were induced by synergetic factors such as high temperature and light (Qiu *et al.*, 2011). SA pre-treatment in wheat not only improved the activity of protein kinase, but it also decreased the degradation of D1 protein during the heat and high light stress, and it also accelerated the recovery of D1 protein levels until the stress was removed. These findings show that SA pre-treatment of wheat leaves will greatly reduce PSII damage caused by heat and high light tension, speeding up photosynthesis restoration (Zhao *et al.* 2011). When exposed to chilling conditions, SA application results in improved photosynthesis in Dendrobium officinale. The consistency of PSII and D1 proteins has increased, although the stability of the chloroplast membrane has been maintained (Huang *et al.*, 2016).

SA mediated Antioxidant Activity

ROS function as a secondary messenger and participate in several developmental and defence responses to stresses in plants at optimal levels (Baxter *et al.*, 2013; Czarnocka and Karpiski, 2018; Farooq *et al.*, 2019). However, they tend to disrupt cell metabolism and other physiological processes in crop plants as their abundance increases under stress conditions. In general, plants stimulate their inborn resistance mechanisms, such as antioxidant enzymes to maintain a balance between ROS generation and quenching. Excess ROS have been shown to have lethal effects on tissues that have been exposed to salt stress (Foyer *et al.* 2017). SOD, CAT, APX, and GPX are among the main enzymatic antioxidant resistance mechanisms in plants (Sharma *et al.*, 2012; Mekawy *et al.*, 2018b; Yassin *et al.*, 2019).

Recent research has found a correlation between ROS accumulation and SA acid-mediated defence signalling in response to various stresses (Brosché *et al.*, 2014; Xu and Brosché, 2014; Nazar *et al.*, 2017). Application of SA enhanced the activity of catalase (CAT), peroxidase (POX), and superoxide dismutase (SOD) in mung bean under aluminum (Al) stress (Ali, 2017), in soybean under arsenic stress (Chandrakar *et al.*, 2016), and in maize under chromium stress (Islam *et al.*, 2016). In Arachis hypogeal cultivars, osmotic stress was created when applying an herbicide known as Basagran®. However, SA application enhanced the content of total phenols, sugars, and the activity of enzymatic antioxidants and regulates osmotic pressure. These findings reflect SA's protective function in the detoxification of Basagran® (Radwan *et al.*, 2019).

The synthesis of non-enzymatic antioxidants such as proline, glycine betaine, glutathione, ascorbic acid, and carotenoids is also induced by SA. Under NaCl stress, SA increased glutathione, ascorbate, dehydro-ascorbate, and oxidized glutathione levels, which act as antioxidants and minimise hydrogen peroxide levels (Yan *et al.*, 2018). Under salinity, supplementing with SA improved glycine betaine, proline, and carbohydrates, resulting in osmo-protection and ionic equilibrium (Farhangi-Abriz and Ghassemi-Golezani, 2018). Externally applied SA increases the rate of SOD, CAT, APX, and DHAR and GR operation, as well as the content of proline, GB, and sugars in Vigna angularis under salt stress (Ahanger *et al.*, 2020). Similarly, Singh and Tripathi (2019), found that SA application helps plants resist osmotic pressure by growing sugar levels and rendering them salt resistant.

SA's flowering-inducing action

The role of SA in flowering control has long been recognized. Initially, it was discovered that 4µM SA encourages the development of flower buds from tobacco callus (Lee and Skoog, 1965). SA later identified the phloem-transmittable factor secreted in aphid honeydew. It was responsible for flowering in Lemna gibba plants that were subjected to a non-photo-inductive light cycle (Cleland and Ajami, 1974). Flowering is also induced by SA (3-10 M) in the Lemnaceae family, including long day (LD), short day (SD), and photoperiod-insensitive types (Khurana and Cleland, 1992). Experiments have shown that thermogenic plant inflorescences produce higher levels of endogenous SA (Raskin *et al.*, 1990). SA levels in the leaves of non-thermogenic plants like tobacco and Arabidopsis increase 5-fold and 2-fold, respectively, at the beginning of or during the transition to flowering (Yalpani *et al.*, 1993; Abreu and Munne- Bosch, 2009).

Aghdam *et al.*, (2016) discovered that SA treatment improved flowering reduced stress, and extended the post-harvest period. According to Wada *et al.*, (2014), SA increased flowering in Pharbitis zero under nutrient-deficient conditions. Yamada and Takeno, (2014) discovered that treating Pharbitis zero or Japanese morning glory with SA improved flowering by increasing expression of the PnFT2 gene in nutritionally deficient conditions. Continuous SA exposure on Gladiolus flowers improved flowering, blooming rate, vase survival, and thus delayed senescence by reducing ion leakage in petals (Hatamzadeh *et al.*, 2012). After applying various doses of SA, the number of female flowers 3in cucumbers was also increased (Sultan *et al.*, 2016).

A crucial connection between SA and flowering has recently been discovered in sunflowers. When expressed constitutively in Arabidopsis, the transcription factor HAHB10, which belongs to the HD-Zip II family, induces flowering by upregulating specific flowering transfer genes and repressing genes linked to biotic stress. Surprisingly, expression of HAHB10 is caused by SA therapy and infection with P. syringae (Dezar *et al.*, 2011). Flowering in Arabidopsis is regulated by a complex network of pathways, and the role of several genes has been identified. CONSTANS regulates the photoperiod pathway (CO). FLOWERING LOCUS C (FLC) is a flowering repressor gene that combines the autonomous and vernalization pathways. Two integrators, FLOWERING LOCUS T (FT) and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1, converge on a limited number of integrators (SOC1). The photoperiod and autonomous pathways are related by the SOC1 gene, which encodes a MADS-box protein that is regulated by CO and suppressed by FLC (Mouradov *et al.*, 2002). Latest studies have shown that SA is active in controlling these genes' transcription (Martı'nez *et al.*, 2004).

Senescence

SA requirement for senescence regulation

In addition to the significant role of SA in cell redox homeostasis and photosynthesis, the Senescence SA necessity for senescence control is also involved in senescence regulation. Senescence is characterized by a decrease in photosynthetic activity due to a lack of antioxidant ability and increased ROS levels. Senescence is characterized by significant changes in gene expression, and SA plays a significant role in this. Several SAG transcripts, such as SAG12, are significantly reduced in SA-deficient Arabidopsis plants (Morris *et al.*, 2000). In Arabidopsis, SA also promotes the expression of senescence-related genes. The genes involved are aVPE, cVPE, WRKY6, WRKY53, and SEN1. They encode two vacuolar synthesis enzymes, two transcription factors, and a protease (Robatzek and Somssich, 2001; Miao *et al.*, 2004; Schenk *et al.*, 2005).

Autophagy induction by SA during developmental leaf senescence

The induction of autophagy by SA during developmental leaf senescence is critical for plant growth, particularly during senescence and the defense response (Kwon and Park, 2008). The role of autophagy in the senescence process was discovered by analyzing Arabidopsis knock-out plants affected in different ATG (autophagy) genes. In revised literature, Bassham *et al.*, (2006) reported that under nutrient-rich conditions, some plants display an improved senescence phenotype. In senescent tissues, the autophagy genes ATG5, ATG8, and ATG12 are strongly expressed (Wagstaff *et al.*, 2009). Autophagy, which is induced by SA, regulates an acyl-CoA-binding protein (ACBP3), which binds phosphatidylcholine and phosphatidylethanolamine. Interfering with the development of the ATG5–phosphatidylethanolamine complex and, as a result, disrupting the formation of autophagosomes and subsequent degradation of ATG8 (Xiao and Chye, 2010; Xiao *et al.*, 2010).

Table 1. Summary on the role of exogenous applied salicylic acid in plants when subjected to NaCl stress.

Salt stress NaCl Dose (s)	Plant	Concentration (SA)	SA induced effect	Reference (s)
1.2, 4, 8 and 12 dS m^{-1}	*Vigna radiata*	100, 200 and300 mg L^{-1}	Improved growth and productivity by enhanced nitrogen metabolism by increasing NRA, NiRA, & other proteins	Akhtar *et al.*, (2013)
90, 120, 150 and 200 mM	*Vicia faba*	0.25, 0.5 and 1 mM	Seed priming with SA improved and enhanced germination traits under various stress levels	Anaya *et al.*, (2018)
2-12 dS m^{-1}	*Hordeum vulgare*	0.5, 1.0, 1.5, and 2.0 mM	Induced Salinity Tolerance through Manipulation of Ion Distribution Rather than Ion Accumulation in barley plants	Pirasteh-Anosheh *et al.*, (2017)
40 and 80mM	*Egletes viscosa*	1.0 mM	modulated primary and volatile metabolites to alleviate salt stress induced photosynthesis impairment.	Batista et al., (2019)
100 and 200 mM	*Raphanus sativus*	2 and 5mM	SA Induced Photosynthetic Adaptability of *Raphanus sativus to Salt Stress by enhanced Antioxidant acitvity*	Bukhat *et al.*, (2020)
3, 6 and 9 dS m^{-1}	*Vigna radiata*	0.5, 1, and 1.5 mM	Regulated photosynthetic electron transfer and stomatal conductance of mung bean under salinity stress	Lotfi *et al.*, (2020)
50 mM NaCl	*Vigna radiata*	0.5 mM	Salicylic Acid and Sulphur- Enhanced Defence Systems, Nitrogen Metabolism, Photosynthetic, and Growth Potential of Mungbean (Vigna radiata) Under Salt Stress	Hussain *et al.*, (2020)

Cross-talks with other phytohormones

By cross-talking with auxins, gibberellins, abscisic acid, jasmonic acid, and ethylene hormones, SA plays a diversified role in plant growth processes and hence minimizes stressful situations (Khan *et al.*, 2014; Zhang and Li, 2019; Arif, *et al.*, 2020).

The discovery that the transcription factors OBP1, OBP2, and OBP3 of SA-inducible DOF are also receptive to AUXs (Kang and Singh, 2000) and provides a clear link between the signalling pathways of SA and AUX. Wheat seedlings treated with 50 M SA showed a higher rate of cell division. It is associated with an increase in endogenous AUX indole acetic acid levels (Shakirova *et al.*, 2003). The Arabidopsis cpr5, cpr6, and snc1 mutants, which have decreased apical dominance and stunted growth phenotypes similar to AUX deficient plants, have increased endogenous SA levels. This suggests interaction caused by SA with the AUX-mediated responses. In addition, Tryptophan, an IAA biosynthetic pathway intermediate, is implicated in SA-induced pathogenic resistance (Denancé *et al.*, 2013).

In general, during the development of structural acquired resistance, SA is antagonistic to ABA (SAR). ABA's exogenous application hampered SAR induction, while SAR activation by SA suppressed ABA signalling by ABA (Yasuda *et al.*, 2008). Furthermore, high endogenous SA concentrations improved salt tolerance in two ABA-sensitive mutants (aba3 and siz1) (Asensi-Fabado and Munne-Bosch, 2011; Miura *et al.*, 2011), suggesting that ABA signalling suppression is necessary for salt tolerance. Exogenous gibberellins added under NaCl (150 mM) stress slightly improved SA-deficient sid mutant germination (AlonsoRamirez *et al.*, 2009), implying that gibberellins would compensate for SA deficiency.

SA prevented the decrease of auxin and cytokinin in wheat to promote growth while retaining high levels of ABA to boost the tolerance of plant salt (Shakirova, *et al.*, 2003). SA treatment downregulated ABA biosynthesis genes in Limonium bicolor, while upregulated Ka biosynthesis genes increased seed germination by preserving a favorable GA/ABA equilibrium under saline tension (Liu *et al.*, 2019). It indicates the resistance of SA regulated plant salt resistance by interactions with other plant hormones.

CONCLUSION

This analysis concludes that SA functions as a potent phytohormone when used against environmental signals. Beyond the defensive response in plant immunity, it controls a number of plant growth production responses, especially at low concentrations. It promotes seed germination, photosynthesis, plant growth and production, and flowering, among other physiological processes. It also improves the activity of ROS-scavenging enzymes. Thus, cellular homeostasis is maintained and salinity stress tolerance is provided. Further studies are needed to establish molecular and signalling pathways of abiotic stress tolerance due to the role of SA in abiotic stress management.

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CONFLICTS OF INTEREST

All authors have declared that they do not have any conflict of interest for publishing this research.

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