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Salicylic Acid: An All-Rounder in Regulating Abiotic Stress Responses in Plants

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Abstract

Salicylic acid (SA) is an endogenous growth regulator of phenolic nature and also a signaling molecule, which participates in the regulation of physiological processes in plants such as growth, photosynthesis, and other metabolic processes. Several studies support a major role of SA in modulating the plant response to various abiotic stresses. It is a well-founded fact that SA potentially generates a wide array of metabolic responses in plants and also affects plant-water relations. This molecule also found to be very active in mitigating oxidative stress under adverse environmental conditions. Since abiotic stress remained the greatest constraints for crop production worldwide, finding effective approaches is an important task for plant biologists. Hence, understanding the physiological role of SA would help in developing abiotic stress tolerance in plants. In this chapter, we will shed light on the recent progress on the regulatory role of SA in mitigating abiotic stress.

Keywords: abiotic stress, antioxidant defense, oxidative stress, phytohormones, ROS signaling

1. Introduction

Abiotic stresses are a potential threat to agricultural productivity all over the world. Anthropogenic activities provoked the degradation of the agricultural system. Drought, excess soil salinity, extreme high, and low temperatures, metals/metalloids, ozone, UV-B radiation, nutrient (deficiency and excess) are the abiotic stresses which have increased many more times than previous due to anthropogenic activities [1, 2]. It has been projected that abiotic stresses may adversely affect 70% yield of staple food crops and decrease overall crop production by more than 50% [3, 4]. Thus, to improve plant performance and to reduce the loss of productivity

caused by abiotic stress is vital. This can be implemented through various approaches and one of those is the application of exogenous phytoprotectant molecule.

Salicylic acid or orthohydroxy benzoic acid is ubiquitously distributed plant growth regulator [5]. Salicylic acid has positive effects on plant growth and developmental processes [5–7]. Research findings demonstrated its roles in seed germination, glycolysis, flowering, fruit yield [8], ion uptake and transport [9], photosynthetic rate, stomatal conductance (g_s), and in transpiration [10]. Salicylic acid can modulate antioxidant defense system thereby decreasing oxidative stress [11]. Photosynthesis, nitrogen metabolism, proline (Pro) metabolism, production of glycinebetaine (GB), and plant-water relations in abiotic stress affected plants were regulated by SA [12–14]. Induction of defense-related genes and stress resistance in biotic stressed plants have also been reported [15]. Moreover, exogenously applied SA showed putative positive effects on stressed plants [16–20]. Salicylic acid induced genes encoding chaperone, heat shock proteins (HSPs), antioxidants, and secondary metabolites of different types. Moreover, SA was involved in mitogen-activated protein kinase (MAPK) regulation, and in the expression [21]. There is no doubt about the vital roles of SA under abiotic stress condition. So, we will review and cover the area regarding the biosynthesis, involvement, and role of salicylic acid on abiotic stress affected plants.

2. Biosynthesis and metabolism of SA

Salicylic acid biosynthesis can occur through two distinct pathways viz. isochorismate (IC) pathway and phenylalanine ammonia-lyase (PAL) pathway (**Figure 1**). Both IC and PAL pathways are started with chorismic acid. Chorismic acid is the end product derived from the shikimic acid pathway in plastid [22–24]. Chorismic acid is converted to IC by isochorismate synthase (ICS) as reported in several plant species [25–27]. Isochorismate pyruvate lyase (IPL) supposed to catalyze the conversion of IC to SA (but the mechanism is not clear) [28].

In PAL pathway, deamination of phenylalanine is accomplished by the activity of PAL which generates *trans*-cinnamic acid. *Trans*-cinnamic acid is converted to intermediate product *ortho*-coumaric acid or producing the benzoic acid which later on produces SA [29–31].

After biosynthesis, SA can be modified into different other forms. Glucosylation of SA generates salicyloyl glucose ester (SGE) and salicylic acid 2-O- β -glucoside (SAG) where the activity of UDP-glucosyltransferase is involved [32]. The SAG can be stored in the vacuole. Methylation of SA is occurred by SAM-dependent carboxyl methyltransferase to produce methyl salicylate (MeSA) [33]. After production, MeSA is transported to different parts of the plant. Through amino acid conjugation with SA, salicyloyl-L-aspartic acid (SA-Asp) generates (GH3-like phytohormone amino acid synthetase is proposed enzyme catalyze this reaction). SA-Asp can undergo through further catabolism [34]. The conversion of SA to SA-2-sulfonate is proposed to catalyze by sulfotransferase and this process is termed as sulfonation [35]. Hydroxylation of SA is responsible for the production of 2,5-dihydroxybenzoate (Gentisic acid) but the enzyme is unknown [36, 37].

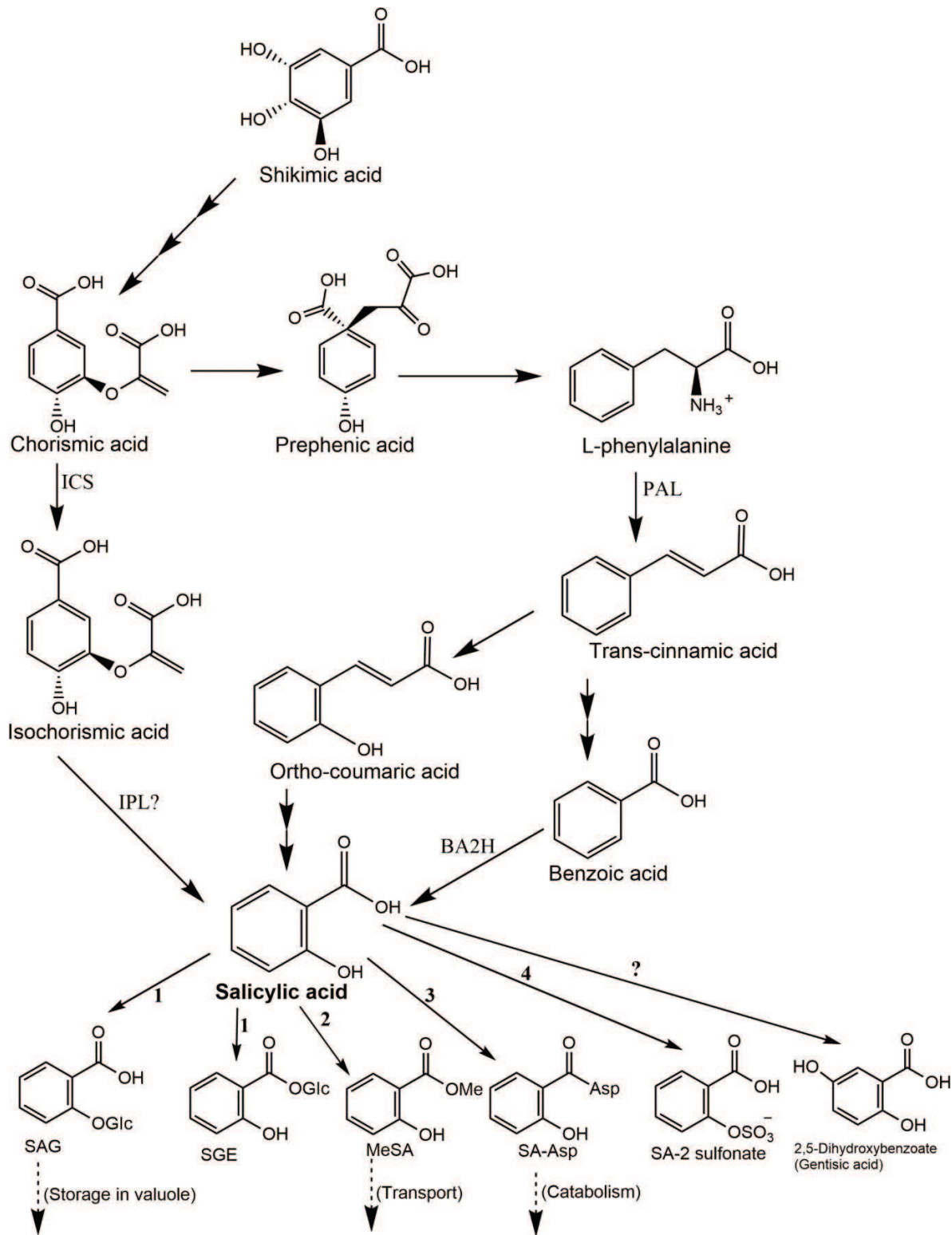


Figure 1. Proposed pathways for SA biosynthesis and metabolism. Biosynthesis of SA is occurred by isochorismate (IC) or phenylalanine ammonia-lyase (PAL) pathways. Salicylic acid is also metabolized into different forms. Isochorismate synthase (ICS), BA2H (benzoicacid-2-hydroxylase), IPL (isochorismate pyruvate-lyase); MeSA (methylsalicylate), SA-Asp (salicyloyl-L-aspartic acid), SAG (salicylic acid 2-O- β -glucoside), SGE (salicyloyl glucose ester) are involved in either or biosynthesis or metabolic pathway of SA. Here, 1 indicates UDP-glucosyltransferase, 2 indicates SAM-dependent carboxyl methyltransferase, 3 indicates GH3-like phytohormone amino acid synthetase, and 4 indicates sulfotransferase.

Modifications of SA often render it inactive but these modifications are also related to accumulation, function, and/or mobility. Glucosylation inactivates SA and allows vacuolar storage. Methylation inactivates SA and increases its membrane permeability, volatility which is vital for long-distance transport of this defense signal. Amino acid conjugation of SA is involved in SA catabolism [37].

3. Salicylic acid and abiotic stress tolerance

As a phytohormone, the role of SA in regulating plant growth and development is well known. The role of SA in mitigating abiotic stress has widely been studied since last few decades (Tables 1–4). A large volume of research reports indicate that both endogenous SA synthesis and exogenous application enhance plants tolerance to salinity [38–42], drought [43–45], extreme temperature [46–49], toxic metal and metalloids [50–53], and others [54–58]. Exogenous SA showed enhanced plant growth, photosynthesis, and decreased ROS production under various abiotic stresses (Tables 1–4 and Figure 2).

3.1. Salinity

Among the prevailing catastrophic abiotic stresses, salinity or salt stress can be considered as the most devastating one. It shows enormous negative effects, both direct and indirect, on morphological, physiological and biochemical attributes of plants. When plants are exposed to

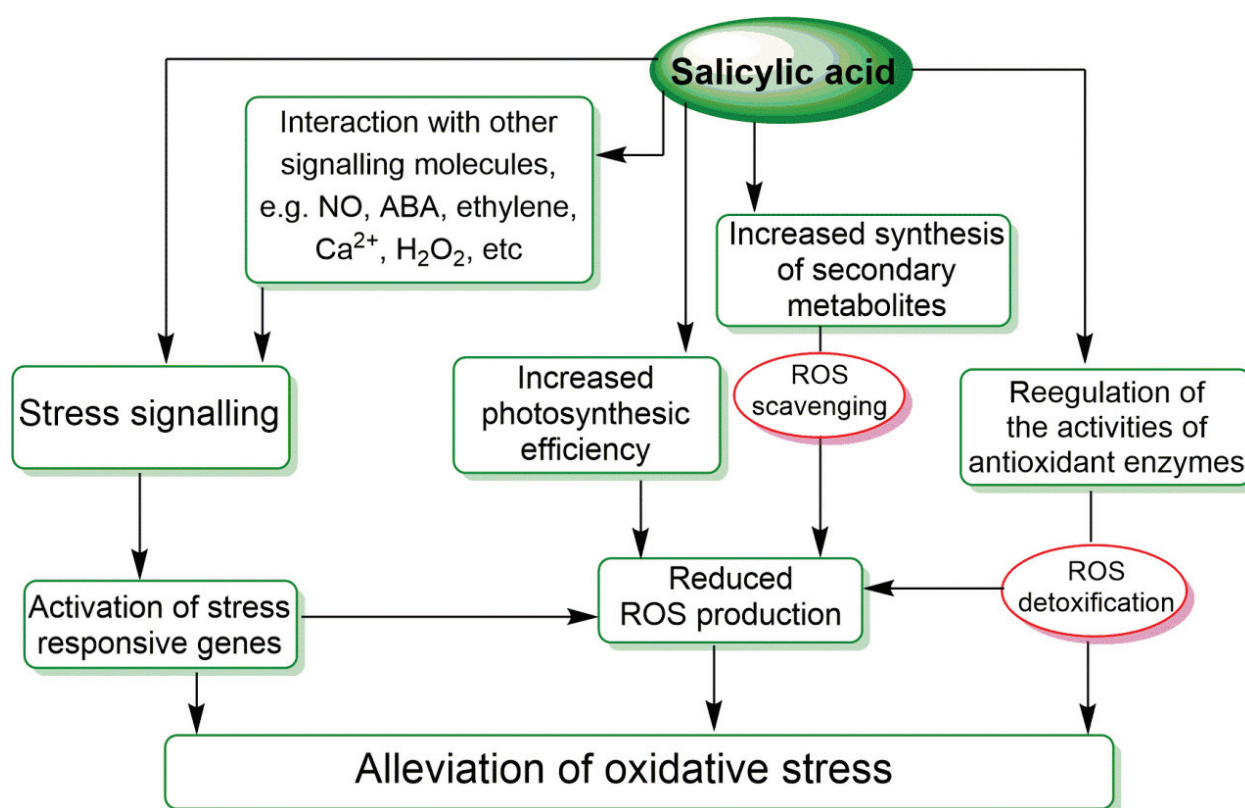


Figure 2. Some possible ways of SA-induced oxidative stress tolerance to plants.

Plant species	Salinity level	Effect of salinity	SA application	Protective effects	Reference
<i>V. radiata</i> L. cv. Pusa Vishal	100 mM NaCl, 20 d	<ul style="list-style-type: none"> • TBARS and H₂O₂ contents increased 2.5 and 4-times respectively, compared to control • Na⁺ and Cl⁻ accumulation increased more than 3-times compared to control • Activity of GR, contents of GSH and GSSG increased compared to control • Net photosynthesis, g_{sr}, C_i, carboxylation efficiency, WUE, and plant dry mass decreased compared to control • Content of methionine, GB, and ethylene evolution increased 	Spraying 0.5 mM SA, 15 d	<ul style="list-style-type: none"> • TBARS and H₂O₂ contents decreased 1.5-times and 2.5-times respectively, compared to salt-treated plant • Reduced Cl⁻ and Na⁺ contents by 50 and 39.8% compared to salt-treated plant • GR activity and GSH content increased but GSSG content decreased compared to stressed plant • P_{iv}, g_{sr}, C_i, carboxylation efficiency, WUE, and plant dry mass decreased compared to salt-treated plant • Content of methionine, GB and ethylene evolution decreased compared to stressed plant 	Khan et al. [17]
<i>T. aestivum</i> cv. S-24 and MH-97	150 mM NaCl, 30 d	<ul style="list-style-type: none"> • Reduced shoot fresh and dry mass, and leaf area in both cultivars • Reduced grain yield plant⁻¹, 100-grain weight and number of spikelets in both cultivars • Reduced the net CO₂ assimilation rate (A), transpiration rate (E), g_{sr}, C_i and WUE in both cultivars 	0.25, 0.50, 0.75 and 1 mM SA in growth media, 30 d	<ul style="list-style-type: none"> • Increased fresh and dry masses of both shoot and root at 0.25 mM SA under saline condition • 0.25 mM SA reduced salt-induced damage in grain yield, 100-grain weight and number of grains of S-24 but, in case of MH-97 grain yield slightly improved with 0.50 mM SA application • SA increased A in S-24 at 0.25 mM concentration but in MH-97 at higher concentrations (0.75 and 1 mM) 	Arfan et al. [59]
<i>L. esculenta</i> cv. DPL-62	100 mM NaCl, 10 d	<ul style="list-style-type: none"> • Decreased germination percentage, shoot length, root length, FW and DW • Free Pro and GB content increased in both shoot and root • Activities of P-5-CR and γ-glutamyl kinase increased but Pro oxidase decreased 	0.5 mM SA in growth media, 10 d	<ul style="list-style-type: none"> • Improved germination percentage, shoot length, root length, FW and DW compared to salt stresses plants • Increased rate of free Pr and GB content was higher in shoot than root under salt stress • Activities of P-5-CR and γ-glutamyl kinase further increased and Pro oxidase decreased 	Misra and Saxena [61]

Plant species	Salinity level	Effect of salinity	SA application	Protective effects	Reference
<i>G. jamesonii</i> L. cv. Amaretto	100 mM NaCl, 15 d	<ul style="list-style-type: none"> • EL and MDA content increased • Activities of SOD, POD, CAT and APX increased • Higher Pro content 	0.5 mM SA pretreatment, 2 d	<ul style="list-style-type: none"> • EL and MDA content decreased • Activities of SOD, POD, CAT and APX further increased • Lower Pro content 	Kumara et al. [39]
<i>B. juncea</i> L. cv Pusa Jai Kisan	100 mM NaCl, 30 d	<ul style="list-style-type: none"> • TBARS and H₂O₂ contents increased 2.5-times and 3.8-times respectively, compared to control • Increased Na⁺ and Cl⁻ contents in leaves • Increased activities of DHAR, APX and GR by 30, 217 and 79%, respectively compared to control • Activities of ATPS and Serine acetyl transferase (SAT) and cystein (Cys) contents increased by 30, 23, and 70%, respectively, but S content decreased by 32% compared to control • Increased DHA, GSH, and GSSG contents but, decreased AsA content • Reduced net photosynthesis, g_s and C_i by 40.0, 26.4, and 41.3%, respectively, compared to control 	0.5 mM SA spray, 15 d	<ul style="list-style-type: none"> • TBARS and H₂O₂ contents were decreased significantly • Reduced Na⁺ content by 36% and Cl⁻ content by half compared to salt treated plants • Activities of DHAR, APX and GR further increased by 54, 248 and 111%, respectively compared to control • Activities of ATPS and SAT, and contents of Cys and S increased by 87, 76, 128, and 63% respectively, compared to control • GSH content further increased while DHA and GSSG both were reduced, AsA content increased • Limited the decreases in the above characteristics to 22, 19 and 25% respectively, compared to control 	Nazar et al. [41]
<i>S. lycopersicum</i> Mill. L. cv. Rio Fuego	100 mM NaCl	<ul style="list-style-type: none"> • Higher accumulation of ABA in both leaves and root • Ethylene production increased • Reduced net CO₂ fixation rate 	Pretreated with 0.01 μM and 100 μM SA, 21 d	<ul style="list-style-type: none"> • Lower accumulation of ABA compared to stressed plants • Prevented higher production of ethylene • Net CO₂ fixation rate enhanced 	Horváth et al. [62]
<i>Hordeum vulgare</i> L. cv. Gustoe	150 mM NaCl, 14 d	<ul style="list-style-type: none"> • Shoot FW and height decreased by 30 and 36% respectively, compared to control • Photosynthetic pigment contents decreased by 57% compared to control • MDA content increased by 40% compared to control 	50 μM SA, 14 d	<ul style="list-style-type: none"> • Shoot FW and height increased compared to NaCl treated plants • Photosynthetic pigment contents decreased by only 39% compared to control • MDA content was lower compared to salt-stressed plants • Na⁺ content decreased and K⁺ content increased 	Fayez and Bazaid [63]

Plant species	Salinity level	Effect of salinity	SA application	Protective effects	Reference
		<ul style="list-style-type: none"> • Na⁺ content increased and K⁺ content decreased compared to control 		<ul style="list-style-type: none"> • compared to plants exposed to salt stress 	
<i>V. radiata</i> L. cvs. Pusa Vishal and T44	50 mM NaCl, 30 d	<ul style="list-style-type: none"> • Increased root and shoot Na⁺ and Cl⁻ contents • Decreased NR activity and N content • Leaf ATPS activity, S, H₂O₂, MDA contents and EL increased • Decreased water potential and osmotic potential by 69 and 52% in Pusa Vishal and 70 and 69% in T44, respectively compared to control • SOD, APX, GR activities and GSH, GSSG contents increased • g_s, C_i and chl fluorescence decreased 	0.5 mM SA spray, 15 d	<ul style="list-style-type: none"> • Reduced root and shoot Na⁺ and Cl⁻ contents • Increased NR activity and N content • Leaf ATPS activity and S content further increased, but H₂O₂, MDA contents, and EL decreased • Enhanced the water and osmotic potential by 54 and 34% in Pusa Vishal and 33 and 15% in T44 in comparison to control • SOD activity and GSSG content decreased, but APX and GR activities and GSH content further increased • g_s, C_i, and chl fluorescence increased 	Nazar et al. [12]
<i>Torreya grandis</i>	0.4% NaCl, 60 d	<ul style="list-style-type: none"> • Reduced the dry mass of shoots and roots by 29 and 25%, respectively • RWC decreased by 16.70% but Pro content increased • P_{tr}, transpiration rate (T_r) and g_s increased but C_i decreased • Chlorophyll content decreased by 24% • Activities of SOD, CAT, and POD decreased markedly • EL and MDA content increased 	0.5 mM SA, 30 d	<ul style="list-style-type: none"> • Increased the dry mass of the shoots and roots by 16.8 and 18.2%, respectively • Both RWC and Pro content increased compared to stressed plants • P_{tr}, T_r, and g_s decreased and C_i increased • Reduced the decrease of chl content by 17% • Increased the activities of SOD, CAT, and POD by 13, 38, and 19%, respectively • Reduced the EL rate and MDA content 	Li et al. [64]
<i>S. lycopersicum</i> cv. Rio Fuego	100 mM NaCl, 10 d	<ul style="list-style-type: none"> • Water potential decreased and root length increased • Decreased Chl content and increased MDA content • ABA accumulation decreased in shoot but increased in root 	Pretreated with 0.1 and 10 μM SA, 21 d	<ul style="list-style-type: none"> • Water potential increased and root length decreased • Improved Chl content and reduced MDA content than stressed one • ABA accumulation increased in shoot but decreased in root 	Szepesi et al. [38]
<i>A. thaliana</i>	100 mM NaCl, 14 d	<ul style="list-style-type: none"> • Reduced FW, DW and water content • Increased shoot Na⁺ and reduced K⁺ contents 	50 μM SA pretreatment, 1 h	<ul style="list-style-type: none"> • Improved FW, DW and water content • Decreased shoot Na⁺ and enhanced K⁺ contents 	Jayakannan et al. [65]

Plant species	Salinity level	Effect of salinity	SA application	Protective effects	Reference
<i>Medicago sativa</i> cv. Aragon	200 mM, 12 d	<ul style="list-style-type: none"> Reduced the F_V/F_M ratio by 15% Decreased the nodule mass about 60% Activities of CAT, APX and GR reduced but SOD, POX, and DHAR increased 	Pretreated with 0.1 and 0.5 mM, 2 d	<ul style="list-style-type: none"> Reduced the F_V/F_M ratio by only 2% Reduced the decreasing of the nodule mass Only CAT activity further reduced, but the activities of APX, GR, SOD, POX and DHAR further increased 	Palma et al. [20]
<i>T. aestivum</i> L. cv. Yumai 34	250 mM NaCl, 3 d	<ul style="list-style-type: none"> GSH content increased but AsA content decreased 	0.5 mM SA, 3 d	<ul style="list-style-type: none"> GSH content further increased along with AsA content 	Li et al. [66]
<i>Z. mays</i> L., Hamidiye F1	40 mM NaCl, 56 d	<ul style="list-style-type: none"> Membrane permeability and MDA content increased Higher Na^+ and Cl^- concentrations Decreased N and increased P concentrations 	Soil incorporated with 0.5 mM SA, 56 d	<ul style="list-style-type: none"> Ameliorated the deterioration of membrane and reduced MDA content Lower accumulation of Na^+ and Cl^- ions Increased N and decreased P concentrations 	Gunes et al. [60]
<i>S. lycopersicum</i> cv. Rio Fuego	100 mM NaCl, 7 d	<ul style="list-style-type: none"> Activities of APX, GR increased and SOD, CAT decreased Both total ascorbate (AsA) and GSH contents increased in leaves and roots 	Pretreated with 0.1 μM or 100 μM SA, 21 d	<ul style="list-style-type: none"> Activities of APX, GR further increased along with SOD and CAT Further increase of total AsA and GSH 	Tari et al. [42]

Table 1. Salicylic acid-mediated tolerance of different plant species to salinity stress.

salt, they not only face osmotic and ionic stresses, but also water stress and other subsequent stresses may emerge. These ultimately reduce the quality and quantity of the desired yield. However, good news is there are certain species that show some tolerance mechanisms and also some protectants that can help plants to develop tolerance against the salt stress. In the recent era where global warming and rising of sea level are the most alarming issues, these can be promising facts to be considered for further research. There are a number of studies that prove the protective roles of SA against salt stress in many plant species (**Table 1**).

Salicylic acid has been proved to have effective roles on enhancing the germination percentage, shoot and root length, fresh weight (FW) and dry weight (DW) of both shoot and root of plants, uptake of beneficial ions, and also some antioxidant enzyme activities. It also has been proved to reduce the toxic ions uptake and accumulation in plants, membrane damage and transpiration rate, etc. Photosynthesis, growth, and yield were improved and oxidative damages were ameliorated with the application of effective concentrations of SA in different plant species. To demonstrate the role of SA in alleviating the salt stress-induced damage, an experiment was conducted by Arfan et al. [59] with two *Triticum aestivum* varieties, of which one is salt-tolerant (S-24) and another one is salt-sensitive (MH-97). They applied different levels of SA starting from 0.25 to 1.00 mM and created salt stress with 150 mM NaCl in the

Plant species	Drought condition	Effect of drought	SA application	Protective effects	Reference
<i>T. aestivum</i> . cvs. Giza164 and Gemaza 1	Drainage (control, 1/3 field capacity, 2/3 field capacity), 14 d	<ul style="list-style-type: none"> Shoot and root DW and mineral content decreased Increase of sugar, protein in shoot and root of plants 	Seed soaking with 0.5 mM SA	<ul style="list-style-type: none"> Higher accumulation of sugars, protein and mineral Increased DW 	El Tayeb and Ahmed [77]
<i>B. juncea</i> L. cv. BARI Sharisha 11	10 and 20% PEG, 48 h	<ul style="list-style-type: none"> Increased MDA, H₂O₂ and Pro levels Decreased leaf RWC, chl content Decreased AsA content and increased in GSH and GSSG contents GR, APX, GST activities increased DHAR and Gly I activities decreased 	Foliar spray with 50 µM SA	<ul style="list-style-type: none"> Increased leaf RWC, chl, AsA and GSH contents Decreased the GSSG content and maintained a higher ration of GSH/GSSG Increased the activities of MDHAR, DHAR, GR, GPX, CAT, Gly I, and Gly II Decreased H₂O₂ content and lipid peroxidation 	Alam et al. [44]
<i>Cymbopogon flexuosus</i> Steud. Wats. cvs. Neema and Krishna	Water has been reduced to 75 and 50% of field capacity	<ul style="list-style-type: none"> Reduced growth Increased activities of nitrate reductase, carbonic anhydrase, and PEP carboxylase Increased EL, Pro and free amino acid contents 	Foliar application of 10 µM SA	<ul style="list-style-type: none"> Improved growth parameters Modulated the activities of nitrate reductase, carbonic anhydrase, and PEP carboxylase Decreased EL, Pro and free amino acid contents 	Idrees et al. [76]
<i>T. aestivum</i>	PEG 15%, 3 d	Decreased growth	0.5 mM SA, 3 d	<ul style="list-style-type: none"> Overexpressed proteins associated with signal transduction, stress defense, photosynthesis, carbohydrate metabolism, protein metabolism, and energy production Improved growth and drought tolerance in wheat seedlings 	Kang et al. [43]
<i>Satureja hortensis</i>	1/3 and 2/3 of field capacity.	<ul style="list-style-type: none"> Decreased sugar and protein contents Increased Pro and lipid peroxidation 	1.0 and 3.0 mM SA	<ul style="list-style-type: none"> Increased sugar, protein and Pro contents Decreased lipid peroxidation 	Yazdanpanah et al. [78]
<i>C. setosa</i>	Kept in PEG, 4 h	<ul style="list-style-type: none"> Increased leaf rolling 	SA pretreatment, 14 h	<ul style="list-style-type: none"> Increased Pro, sugar, activities of SOD, APX, CAT, GPX and NOX (NADPH oxidase) 	Demiralay et al. [45]

Plant species	Drought condition	Effect of drought	SA application	Protective effects	Reference
<i>Z. mays</i>	Withholding water, 5 d	<ul style="list-style-type: none"> Decreased antioxidant enzyme activities 	100, 150, 200 ppm	<ul style="list-style-type: none"> SA conferred drought tolerance mediated by H₂O₂ Reduced leaf rolling 	Rao et al. [79]
<i>Musa acuminata</i> cv. 'Berangan', AAA	1, 2 and 3% of PEG in vitro, 60 d	<ul style="list-style-type: none"> Slight increase in proliferation rate, FW Decreased RWC and chl content 	1.0, 2.0, and 3.0 mM SA	<ul style="list-style-type: none"> Increased Pro content Reduction in H₂O₂ and MDA contents 	Bidabadi et al. [80]
<i>H. vulgare</i> L. cv Nosrat	40% FC	<ul style="list-style-type: none"> Drought stress decreased the dry mass and net CO₂ assimilation rate 	Spraying with 500 μM SA, 15 d	<ul style="list-style-type: none"> Increased the dry mass, net CO₂ assimilation rate and g_s 	Habibi [81]
<i>O. sativa</i> L. cv. Super-Basmati	Water was reduced to 50% of field capacity	<ul style="list-style-type: none"> Increased H₂O₂, MDA, and relative membrane permeability 	100 mg L ⁻¹ SA	<ul style="list-style-type: none"> Increased tissue water potential, increased synthesis of metabolites and enhanced capacity of the antioxidant system 	Farooq et al. [82]
<i>T. aestivum</i> L.	20 % PEG, 24 h	<ul style="list-style-type: none"> Decreased MSI, increased total soluble sugar and soluble protein content but decreased yield 	10 μM SA, 24 h	<ul style="list-style-type: none"> Increased MSI, increased total soluble sugar and soluble protein content Increased yield 	Khan et al. [73]
<i>T. aestivum</i> L. cv. Hassawi	Reduced water to 60 and 30% field capacity	<ul style="list-style-type: none"> Decreased content of photosynthetic pigments Increased soluble carbohydrate, protein, and Pro Decreased insoluble carbohydrates and proteins Free amino acids were significantly increased in roots, while it was decreased in shoots 	50 ppm SA	<ul style="list-style-type: none"> Stimulated growth, photosynthetic pigments and accumulation of soluble and insoluble carbohydrates and proteins 	Azooz and Youssef [83]

Table 2. Salicylic acid-mediated tolerance of different plant species to drought stress.

growing media. Both SA and NaCl were exposed to plants from the very beginning and data were taken at 30 days after sowing (DAS). Their results showed that at lower concentration

Plant species	Temperature and duration	Damaging effects	SA dose and duration	Protective effects	References
<i>T. aestivum</i>	HT (30°C, 2 h)	<ul style="list-style-type: none"> • Decreased FW • Increased total soluble protein and total RNA contents • Decreased soluble starch synthase activity 	100 mM, foliar spraying, 3 times at 4 h interval	<ul style="list-style-type: none"> • Improved FW • No significant differences in the total soluble protein content • Further increased total RNA content • Increased soluble starch synthase activity 	Kumar et al. [46]
<i>Z. mays</i>	HT (40 ± 1°C, 2 h)	<ul style="list-style-type: none"> • Reduced dry biomass • Increased MDA, H₂O₂ but decreased Pro contents • APX and GR activities increased but CAT and SOD activities decreased 	10–800 µM, foliar spraying, 2 h	<ul style="list-style-type: none"> • Improved dry biomass content • Reduced MDA, H₂O₂ but increased Pro contents • Further improved CAT, SOD and POX activities 	Khanna et al. [48]
<i>L. lycopersicum</i>	HT (32/26°C, 12/12 h, day/night)	<ul style="list-style-type: none"> • Severely reduced germination and plant growth • Negatively affected reproductive parameters • Decreased TSS (total soluble solid), vitamin and lycopene contents 	0.25, 0.5, and 0.75 mM, seed priming	<ul style="list-style-type: none"> • Reduced germination time and increased germination percentage • Improved reproductive parameters. Increased TSS, vitamin and lycopene contents 	Singh and Singh [49]
<i>T. aestivum</i>	HT (40°C, 6 h)	<ul style="list-style-type: none"> • Increased Pro and γ-glutamyl kinase (GK) but reduced Pro oxidase contents • Increased TBARS and H₂O₂ contents • Negatively affected the net photosynthesis, Rubisco activity, chl and WUE of the plant 	0.5 mM, foliar spraying	<ul style="list-style-type: none"> • Further increased Pro and GK and reduced Pro oxidase contents • Reduced TBARS and H₂O₂ contents • Counteracted the negative effects on net photosynthesis, Rubisco activity, chl and WUE of the plant 	Khan et al. [1]
<i>Digitalis trojana</i> Ivanina	HT (45°C, 2 or 4 h)	<ul style="list-style-type: none"> • Lowered CAT and SOD activities • Increased accumulation of Pro • Increased total phenolic and flavonoid contents 	150 µM, pretreatment, 4 h	<ul style="list-style-type: none"> • Increased CAT and SOD activities • Further increased Pro content • Further increased phenolic and flavonoid contents 	Cingoz and Gurel [47]
<i>Vitis vinifera</i>	HT (43°C, 5 h)	<ul style="list-style-type: none"> • Sharply declined P_n and g_s • Lowered Rubisco activity 	100 µM SA, pretreatment, 24 h	<ul style="list-style-type: none"> • Alleviated the harmful effect on P_n • Counteracted the negative effect on Rubisco activation state 	Wang et al. [95]

Plant species	Temperature and duration	Damaging effects	SA dose and duration	Protective effects	References
<i>Matricaria chamomila</i>	HT, Min (10.1–28.2°C), Max (21–44°C), 8 months	<ul style="list-style-type: none"> Reduced plant height, capitol diameter, fresh flower weight, dried flower weight etc. Decreased total chl content Essential oil content was not significantly affected 	1, 10, 25 and 100 mg L ⁻¹ , foliar spraying	<ul style="list-style-type: none"> Improved plant height, capitol diameter, fresh flower weight, dried flower weight etc. Increased total Chl content Improved essential oil content 	Ghasemi et al. [96]
<i>Cucumis sativa</i>	HT (40°C, 36 h)	<ul style="list-style-type: none"> Highly increased EL Increased H₂O₂ and TBARS contents Improved SOD, CAT, DHAR, GPX, APX and GR activities 	1 mM SA, foliar spraying, 12 h	<ul style="list-style-type: none"> Decreased EL Reduced H₂O₂ and TBARS contents Improved SOD, DHAR, GPX, APX and GR activities but inhibited CAT activity 	Shi et al. [97]
<i>B. juncea</i>	HT (30 or 40°C, 24 h)	<ul style="list-style-type: none"> Decreased root length, shoot length, FW and DM of the plant Decreased P_{iv}, g_{sv}, C_{iv}, WUE and SPAD value Increased activities of CAT, POD SOD, and Pro accumulation Decreased N, P, K contents in leaves 	10 μM, foliar spraying	<ul style="list-style-type: none"> Root length, shoot length, DW and FW of plant increased Increased P_{iv}, g_{sv}, C_{iv}, WUE and SPAD value Further enhancement of CAT, POD SOD, and Pro accumulation Improved N, P, K contents in leaves 	Hayat et al. [98]
<i>Musa acuminata</i>	Chilling (5°C, 3 d)	<ul style="list-style-type: none"> Reduced SOD, CAT, APX activities but improved POX activity Increased accumulation of H₂O₂ 	0.5 mM, pretreatment, 1 d	<ul style="list-style-type: none"> Increased SOD, CAT and APX activities but unaffected POX activity Decreased overproduced H₂O₂ 	Kang et al. [99]
<i>T. aestivum</i>	Chilling (3°C, 48–72 h)	<ul style="list-style-type: none"> Reduced chl, CO₂ assimilation and rate of respiration RuBisCO activity decreased Decreased SOD Increased glycolate oxidase (GO) and CAT activities Highest MDA content found 	500 μM, foliar spraying, 24 h	<ul style="list-style-type: none"> Improved Chl content and rubisco activity Enhanced CAT, APX, POX, and glycolate oxidase (GO) activities but GR activity found not affected Reduced MDA content 	Yordanova and Popova [100]
<i>V. vinifera</i>	HT (38 ± 0.5°C, 12 h)	<ul style="list-style-type: none"> Reduced H⁺ and Ca²⁺-ATPase activities The appearance of cerium phosphate grain found 	100 μM, pretreatment, 6 h	<ul style="list-style-type: none"> Increased H⁺ and Ca²⁺-ATPase activities Remained cerium phosphate grain 	Liu et al. [101]

Plant species	Temperature and duration	Damaging effects	SA dose and duration	Protective effects	References
<i>V. vinifera</i>	Freezing (−3°C, 3 h) and HT (44°C, 3 h)	<ul style="list-style-type: none"> • Increased EL and TBARS content • Decreased activities of GR, APX, MDHAR and DHAR • Increased AsA/GSH ratio • Reduced cytosolic Ca²⁺ homeostasis 	2 μM, pretreatment, 1, 3, 6, or 12 h	<ul style="list-style-type: none"> • Reduced EL and TBARS content • Increased activities of GR, APX, MDHAR but reduced DHAR and ratio of AsA/GSH pool • Increased cytosolic Ca²⁺ homeostasis 	Wang and Li [102]
<i>Poa pratensis</i>	HT (46°C, 72 h)	<ul style="list-style-type: none"> • Overproduction of O₂^{•−} and H₂O₂ in a time-dependent manner • Enhanced CAT and SOD activities in a time-dependent manner 	0.1, 0.25, 0.5, 1.0, and 1.5 mM, foliar spraying	<ul style="list-style-type: none"> • Reduced O₂^{•−} and H₂O₂ generation in a time-dependent manner • Significantly increased CAT and SOD activities in a time-dependent manner 	He et al. [103]
<i>O. sativa</i>	HT (27–32°C, night ambient temp)	<ul style="list-style-type: none"> • Spikelet fertility and grain size reduced • Damaged membrane and resulted oxidative damage 	1 mM, foliar spraying	<ul style="list-style-type: none"> • Improved grain characteristics and spikelet fertility • Counteracted oxidative damage • Enhanced antioxidant enzymes activities 	Mohammed and Tarpley [104]
<i>Prunus persica</i>	Chilling (0°C, 28 d)	<ul style="list-style-type: none"> • Increased TBARS content, chilling injury index and decay index • Lowered APX and GR activities and heat shock protein 101 (HSP101) expression 	0.35, 0.7, and 1 mM, 5 min	<ul style="list-style-type: none"> • Maintained optimum level of TBARS content, chilling injury index and decay index • Enhanced reduced to oxidized AsA and GSH ratios • Higher APX and GR activities and heat shock protein 101 (HSP101) expressions 	Wang et al. [105]
<i>Rhododendron</i>	HT (38/30°C (day/night, 6 d)	<ul style="list-style-type: none"> • Resulted in brown, withered and defoliated leaves • Decreased chl and total soluble protein contents • Decreased activity of POX and SOD • MDA and H₂O₂ contents increased 	0.5, 1.0, and 2.0 mM spraying of leaves, 3 d	<ul style="list-style-type: none"> • Lowered the leaf damage rate • Highly declined Chl and total soluble protein contents • Increased POX and SOD activities • Reduced MDA and H₂O₂ contents 	Shen et al. [106]
<i>V. radiata</i>	HT (50°C, 3 h)	<ul style="list-style-type: none"> • Increased lipid peroxidation, H₂O₂, and EL • Reduced CAT, APX, POD and GSH contents 	0.5 and 1 mM, foliar spraying	<ul style="list-style-type: none"> • Decreased lipid peroxidation, H₂O₂, and EL • Increased CAT, APX, POD and GSH contents 	Saleh et al. [107]

Plant species	Temperature and duration	Damaging effects	SA dose and duration	Protective effects	References
<i>Z. mays</i>	Chilling (15°C)	<ul style="list-style-type: none"> Increased endogenous SOD and SA activities Disturbed seedling emergence, root and shoot growth, FW, and DW Lowered RWC and increased membrane permeability 	50, 100, and 150 mg L ⁻¹ , seed priming, 24 h	<ul style="list-style-type: none"> Enhanced defense system and radical scavenging mechanism Improved seedling emergence, root and shoot growth, FW and DW Increased RWC and decreased membrane permeability Highly activated CAT, SOD and APX activities 	Farooq et al. [108]
<i>Brassica</i> sp.	HT (40–55°C, 3 h)	<ul style="list-style-type: none"> Hampered seedling growth Increased EL Increased CAT, POX enzyme activities 	10 and 20 µM, pretreatment, 2 h	<ul style="list-style-type: none"> Conferred protection of membrane Reduced EL Increased FW, DW, and total soluble sugar Increased CAT, POX, and appearance of heat shock proteins 	Kaur et al. [3]

Table 3. Summary of the protective roles of exogenous SA in mitigating extreme temperature-induced damages in different crop plants.

(0.25 mM) SA could reduce the negative effects of salt on the shoot and root FW and DW in tolerant variety, but this was true at higher concentration (0.75 mM) for the sensitive one. However, yield attributes such as grain yield and 100-grain weight were increased in both the varieties at lower concentrations (0.25 and 0.50 mM) SA under salt stress. Similarly, application of SA also increased the water use efficiency (WUE) of those varieties. Similarly, Nazar et al. [12] also chose two such varieties of *Vigna radiata* cvs. Pusa Vishal (salt-tolerant) and T44 (salt-sensitive). They also used different concentrations of SA (0.1, 0.5, and 1.0 mM) against 50 mM NaCl stress and 0.5 mM was concluded as the most suitable concentration for both varieties irrespective of their tolerance ability. At this concentration, *V. radiata* seedlings could reduce the accumulation of toxic Na⁺ and Cl⁻ ions, and increase S and N uptake and nitrate reductase activity. Salicylic acid application also enhanced the water and osmotic potential which was higher in the tolerant one. Stomatal conductance (g_s), intercellular CO₂ concentration (C_i), and chlorophyll (chl) fluorescence were increased along with leaf ATP-sulfurylase activity. However, mainly the reduction of electrolyte leakage (EL), malondialdehyde (MDA), H₂O₂, oxidized glutathione (GSSG) contents, superoxide dismutase (SOD) activity and enhancement of reduced glutathione (GSH) content, and ascorbate peroxidase (APX) and glutathione reductase (GR) activities prove the role of SA in reducing salt-stress damages. Similar results were observed with *V. radiata* seedlings. These seedlings were exposed to 100 mM NaCl at 10 DAS and then was spraying SA (0.5 mM) at 15 DAS. At 30 DAS some parameters were monitored related to gas exchange e.g., net photosynthesis (P_n), g_s , and C_i ; and also carboxylation efficiency, WUE, and plant dry mass [17]. Application of SA increased P_{iv}, g_{sv} , and C_i by 17.9, 19.2, and 23.5%, respectively, under salt stress condition. It also enhanced carboxylation

Plant species	Toxic metals/ metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>O. sativa</i>	As	25 and 50 μM Na_2HAsO_4 , 7 d	<ul style="list-style-type: none"> • Decreased growth and biomass production • Enhanced MDA and H_2O_2 contents 	100 μM , pretreatment, 7d	<ul style="list-style-type: none"> • Reverted the growth inhibition • Reduced oxidative stress by reducing MDA and H_2O_2 contents 	Singh et al. [50]
<i>A. thaliana</i>	As	100 μM Na_2HAsO_4 , 14 d	<ul style="list-style-type: none"> • Decreased plant biomass and chl contents • Increased lipid peroxidation and antioxidant enzymes (APX, CAT, SOD) activities 	250 μM , pretreatment, 14 d	<ul style="list-style-type: none"> • Alleviated the toxic effects of As by restoring growth and chl content • Decreased lipid peroxidation and downregulated activities of APX, CAT, and SOD 	Odjegba [115]
<i>T. aestivum</i>	Cd	0.01, 0.1 and 1 mM $\text{Cd}(\text{OOH})_2$, 24 h	<ul style="list-style-type: none"> • Increased MDA and EL percentage • Reduced FW and DW • Enhanced accumulation of ABA and dehydrins 	50 μM , 24 h, pretreatment	<ul style="list-style-type: none"> • Declined MDA content and EL • Recovered growth • Activated phenylalanine ammonia-lyase (PAL) enzyme activity • Further increased low molecular weight dehydrins by 1.5 folds 	Shakirova et al. [53]
<i>H. vulgare</i>	Cd	15 μM CdCl_2 , 30 min	<ul style="list-style-type: none"> • Reduced root growth markedly • Stimulated activity of LOX, GPX and enhanced accumulation of IAA • Increased generation of ROS in the root apex 	0.25 or 0.5 mM SA, pretreatment, 10 min	<ul style="list-style-type: none"> • Alleviated Cd-induced root growth inhibition • Reduced IAA-induced LOX and GPX activity • Inhibited ROS generation in roots 	Tamás et al. [51]
<i>Lolium perenne</i>	Cd	100 μM CdCl_2 , 14 d	<ul style="list-style-type: none"> • SOD, APX, and CAT activity decreased drastically in both shoots and roots. Increased accumulation of $\text{O}_2^{\bullet-}$, H_2O_2 and increased MDA content 	100, 200, 300, and 400 μM , 14 d	<ul style="list-style-type: none"> • Increased antioxidant enzyme activities and chl content • Increased mineral uptake but decreased Cd uptake • Decreased accumulation of MDA and H_2O_2 	Bai et al. [116]
<i>Phaseolus vulgaris</i>	Cd	0.25, or 0.50 mM CdCl_2 , 2–3 d	<ul style="list-style-type: none"> • Increased Pro and Cd^{2+} ion accumulation • Enhanced EL and lipid peroxidation 	1 mM, foliar spraying, 50, 36, and 22 d	<ul style="list-style-type: none"> • Decreased EL and lipid peroxidation • Reduced activities of antioxidant enzymes, such as SOD, CAT, APX, and GR 	Wael et al. [117]

Plant species	Toxic metals/ metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>T. aestivum</i>	Cd	100, 400 and 1000 μM CdCl ₂ . 2.5 H ₂ O, 30 d	<ul style="list-style-type: none"> • Increased activities of SOD, CAT, APX, and GR • Inhibited root growth and enhanced Cd accumulation in roots • Decreased RWC, chl content, and CO₂ fixation • Increased MDA, H₂O₂ and Pro contents • Altered root and chloroplast ultrastructure 	500 μM , pretreatment, 20 h	<ul style="list-style-type: none"> • Reversed root growth inhibition • Ameliorated the adverse effects on RWC, chl content, and CO₂ fixation • Reduced MDA, H₂O₂ and Pro contents • Recovered chloroplast and root ultrastructures 	Moussa and El-Gamal [118]
<i>Linum usitatissimum</i>	Cd	50 and 100 mM CdCl ₂ , 4 d	<ul style="list-style-type: none"> • Inhibited growth and nutrient absorption • Enhanced MDA content and EL • Reduced total lipid and chl contents 	250 and 1000 μM , presoaking of grains, 8 h	<ul style="list-style-type: none"> • Alleviated growth inhibition and nutrient absorption • Ameliorated the enhanced MDA content and EL • Alleviated the harmful effect on total lipid and Chl contents 	Belkhadi et al. [119]
<i>Phaseolus aureus</i>	Cd	50 and 100 μM CdCl ₂ , 3 or 6 d	<ul style="list-style-type: none"> • Enhanced H₂O₂ and O₂^{•-} production in the root • Increased TBARS content and relative EL rate • Increased antioxidant enzymes such as SOD, CAT and APX activities 	100 μM SA, seed soaking, 16 h	<ul style="list-style-type: none"> • Significantly decreased H₂O₂, O₂^{•-} production in the root • Enhanced TBARS content and relative EL • Further increased SOD, CAT and APX activities 	Zhang et al. [120]
<i>T. aestivum</i>	Cd	500 and 1000 μM CdCl ₂ , 3 d	<ul style="list-style-type: none"> • Reduced growth, chl content, RWC and SOD, CAT, POX activities • Enhanced Pro, EL and Cd contents 	500 μM , seed soaking, 12 h	<ul style="list-style-type: none"> • Mitigated adverse effects of Cd on chl, RWC and SOD, CAT and POX activities • Alleviated damaging effects on EL • Improved leaf anatomy and reduced uptake of Cd 	Agami and Mohamed [121]
<i>Z. mays</i>	Cr	50 mg L ⁻¹ K ₂ Cr ₂ O ₇ , 7 d	<ul style="list-style-type: none"> • Decreased growth, photosynthetic pigments, CHO metabolism 	100 μM L ⁻¹ , foliar application, 15 d	<ul style="list-style-type: none"> • A significant decline in MDA, H₂O₂, Pro and Cr contents 	Islam et al. [52]

Plant species	Toxic metals/ metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>Catharanth roseus</i>	Ni	50, 100, and 150 mg kg ⁻¹ NiSO ₄ ·6H ₂ O	<ul style="list-style-type: none"> Increased MDA, H₂O₂, Pro and Cr contents Decreased CAT but increased SOD and POD activities 	10 μM, foliar spraying, 4 sprays at 10 d intervals from 30 DAS	<ul style="list-style-type: none"> Improved plant growth, photosynthetic pigments Reduced oxidative stress by upregulating antioxidant enzymes (CAT, SOD, POD) activities 	Idrees et al. [122]
<i>B. napus</i>	Ni	0.5 mM NiCl ₂ ·6H ₂ O, 10 d	<ul style="list-style-type: none"> Resulted leaf chlorosis and necrosis Decreased growth and leaf chl content LOX, MDA, H₂O₂, and Pro content increased Reduced CAT, APX and GPX activity 	0.2 mM SA, cotreatment, 10 d	<ul style="list-style-type: none"> Decreased leaf chlorosis and necrosis Improved growth and leaf chl content A significant decline in LOX, MDA, H₂O₂ and Pro contents Increased CAT, APX and GPX activities 	Kazemi et al. [123]
<i>O. sativa</i>	Cu	75 or 150 μM CuSO ₄ , 48 h	<ul style="list-style-type: none"> Highly increased MDA, O₂^{•-}, H₂O₂ contents and LOX activity Reduced Chl and leaf RWC Reduced AsA, GSH, nonprotein thiol and pro contents in roots 	100 μM SA, pretreatment, 24 h	<ul style="list-style-type: none"> Curtailed Cu-induced enhancement of MDA, O₂^{•-}, H₂O₂ contents and LOX activity Increased Chl, leaf RWC, AsA, GSH, nonprotein thiol contents Enhanced antioxidant enzymes (SOD, CAT, APX, GR, GPX, DHAR and GST) activities 	Mostofa and Fujita [124]
<i>Zygophyllum fabago</i>	Pb	0.75 mM Pb (NO ₃) ₂ , 7 d	<ul style="list-style-type: none"> Downregulated CAT, APX, GR but upregulated DHAR activity Increased MDA and EL 	0.5 mM SA, pretreatment, 24 h	<ul style="list-style-type: none"> Increased SOD activity Reduced accumulation of Pb and chl contents 	Lopez-Orenes et al. [125]
<i>T. aestivum</i>	Pb	10, 50, 100, 200 mg L ⁻¹ Pb ²⁺ , 7 d	<ul style="list-style-type: none"> Decreased chl content in a dose-dependent manner 	200 mg L ⁻¹ , cotreatment, 7 d	<ul style="list-style-type: none"> Alleviated the inhibitory effects on Chl and antioxidant 	Song et al. [126]

Plant species	Toxic metals/ metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>P. pratensis</i>	Cd	5,10, or 50 mM CdCl ₂ , 7 d	<ul style="list-style-type: none"> Inhibited APX, CAT, MDA and Pro contents POD, SOD, and soluble sugar contents were affected Reduced growth, chl and nutrient (K, Ca, Fe, Mg) elements Elevated MDA and H₂O₂ contents Increased Cd uptake and accumulation 	500 mM SA, pretreatment, 12 h	<ul style="list-style-type: none"> enzymes activities. Lowered MDA and Pro contents Reduced the adverse effects of Pb on POD, SOD, and soluble sugar contents Increased growth, chl, and nutrient (K, Ca, Fe, Mg) elements Decreased MDA and H₂O₂ contents and Cd uptake Marked increase in SOD, APX, and POD but decreased CAT activity 	Guo et al. [127]
<i>Spinacia oleracea</i>	B	50 mg kg ⁻¹ , H ₃ BO ₃	<ul style="list-style-type: none"> Enhanced B Accumulation in plants Decreased chl and anthocyanin contents Increased MDA, H₂O₂ and stomatal resistance 	0.5 mM kg ⁻¹ , cotreatment	<ul style="list-style-type: none"> Decreased B accumulation Improved chl and anthocyanin contents Influenced antioxidant enzymes activity and stomatal resistance 	Eraslan et al. [128]
<i>Daucus carota</i>	B	25 mg kg ⁻¹ , H ₃ BO ₃	<ul style="list-style-type: none"> Increased storage root diameter Increased oxidative damage as indicated by increased MDA content Lowered chl content 	0.5 mM kg ⁻¹ , cotreatment	<ul style="list-style-type: none"> Enhanced storage root DW Increased anthocyanin and carotenoid contents Controlled metal toxicity and pro accumulation in roots and shoots 	Eraslan et al. [129]
<i>B. juncea</i>	Mn	3.0, 6.0, or 9.0 mM MnCl ₂ , 3 d	<ul style="list-style-type: none"> Decreased growth, photosynthetic pigments, carbonic anhydrase activity, and water relations Increased MDA, H₂O₂, Pro accumulation Elevated antioxidant enzymes (CAT, SOD, POD) activity in a dose-dependent manner 	10 μM, 14 d, foliar application	<ul style="list-style-type: none"> Improved growth, photosynthetic pigments, carbonic anhydrase activity, and water relations Lowered MDA, H₂O₂, and EL in a dose-dependent manner Further accelerated activity of antioxidant enzymes (CAT, SOD, POD) 	Parashar et al. [130]

Plant species	Toxic metals/ metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>C. sativus</i>	Mn	600 μ M MnSO ₄ , 11 d	<ul style="list-style-type: none"> • Caused stunted growth, severe chlorosis, a marked increase in Mn accumulation • Inhibited nutrients (Ca, Mg, Zn) absorption • Increased ROS production and lipid peroxidation 	100 μ M SA, co-treatment, 11 d	<ul style="list-style-type: none"> • Promoted growth and reduced Mn toxicity • Alleviated the effects on nutrients (Ca, Mg, Zn) absorption • Reduced Increased ROS production and lipid peroxidation • Increased SOD, POD, DHAR, GR, ASA and GSH activities but decreased CAT and POX activities 	Shi and Zhu [131]
<i>Glycine max</i>	Al	30 μ M AlCl ₃ , 12 h	<ul style="list-style-type: none"> • Inhibited root elongation • Accelerated SOD, POD, and APX activities in roots • Upregulated the CaM-like protein genes 	10 μ M, cotreatment, 12 h	<ul style="list-style-type: none"> • Restored root growth • Further enhanced SOD and POD activities • Upregulated CaM-like protein genes • Increased cytosolic Ca²⁺ concentration 	Lan et al. [132]
<i>Vallisneria natans</i>	Pb	50 μ M Pb(NO ₃) ₂ , 4 d	<ul style="list-style-type: none"> • Decreased total chl content • Increased MDA, O₂^{•-} H₂O₂ contents • Increased CAT but no significant effect on APX and POD 	10 or 100 μ M, cotreatment, 4 d	<ul style="list-style-type: none"> • Decreased Chl and carotenoid contents • Inhibited the overproduction of MDA, O₂^{•-} and H₂O₂ • Decreased APX but increased CAT, DHAR and POD activities • Decreased NADPH oxidase, nonprotein thiols, AsA 	Wang et al. [133]
<i>Medicago sativa</i>	Hg	10 μ M HgCl ₂ , 24 h	<ul style="list-style-type: none"> • Increased Lipid peroxidation and TBARS accumulation • Slight increase in NADH oxidase, SOD and POD activities • Decreased APX and GR activities • Decreased AsA, GSH, and Pro accumulation 	0.2 mM, pretreatment, 12 h	<ul style="list-style-type: none"> • Increased activities of NADH oxidase, APX, POD, GR but decreased SOD activity • Elevated AsA, GSH and Pro accumulation 	Zhou et al. [134]
<i>B. oleracea</i> var. botrytis	Co, Ni, Cd, Cr, and Pb	0.25 M	<ul style="list-style-type: none"> • Retarded growth 	50 and 100 mM, cotreatment	<ul style="list-style-type: none"> • Reversed all the toxic effects caused by HM except for Cr 	Sinha et al. [135]

Plant species	Toxic metals/metalloids	Doses and duration	Toxic effects	SA doses and duration	Protective effects	References
<i>Pisum sativum</i>	Cd	0.5, 1, 2, and 5 μM CdCl ₂	<ul style="list-style-type: none"> • Increased MDA, nonprotein thiol, EL percentage and Pro contents • Increased POD and SOD activities • Decreased FW, CO₂ fixation, chl content and RuBPC activity • Increased MDA, Pro content, and EL percentage 	500 μM , seed pretreatment, 6 h	<ul style="list-style-type: none"> • In the case of Cr, SA accelerated the toxic effects and the plants died • Restored FW, CO₂ fixation, chl content and RuBPC activity • Alleviated the effects on MDA, Pro contents, and EL percentage 	Popova et al. [136]
<i>Cannabis sativa</i>	Cd	CdCl ₂ . 2.5 H ₂ O at 0, 25, 50, and 100 mg kg ⁻¹ sands	<ul style="list-style-type: none"> • Inhibited plant growth • Slightly reduced photosynthetic capacity • Increased Cd uptake 	500 μM , seed soaking, 6 h	<ul style="list-style-type: none"> • Counteracted growth inhibition • Improved photosynthetic capacity • Reduced Cd uptake • Enhanced SOD and POD activities 	Shi et al. [137]
<i>H. vulgare</i>	Zn ²⁺ , Cu ²⁺ , Mn ²⁺ , Cd ²⁺ , Hg ²⁺ , and Pb ²⁺ , 7 d	0.1, 0.2, 0.5, and 1 mM Zn ²⁺ , Cu ²⁺ , Mn ²⁺ , Cd ²⁺ , Hg ²⁺ , and Pb ²⁺	<ul style="list-style-type: none"> • Inhibitory effects on SOD and CAT at higher dose 	2 mM, cotreatment, 7 d	<ul style="list-style-type: none"> • Alleviated the harmful effects on antioxidant enzymes (CAT, SOD) activities 	Song et al. [138]

Table 4. Summary of the protective roles of SA in mitigating toxic metal/metalloid-induced damages in different crop plants.

efficiency and WUE compared to salt-stressed plants. Plant dry mass was increased by 25.2% under salt condition compared to control plants. Meanwhile, *Zea mays* was tested with different levels of SA under salt stress, and positive roles of SA was demonstrated in ameliorating the membrane damage by reducing MDA content [60]. It can also decrease the accumulation of Na^+ and Cl^- ions and increase uptake of N and P and thus render tolerance to plants against salt stress. Another experiment was conducted with *Lens esculenta*, which included only four with *Lens esculenta*, which included only four treatments: nonsaline control (I), 0.5 mM SA (II), 100 mM NaCl (III), and the combination of 100 mM NaCl + 0.5 mM SA (IV). The results showed that growth parameters: germination (%), shoot and root length, FW and DW were improved in treatment (IV) compared to treatment (III). In addition, SA increased the free Pro and GB content in shoot and also the activities of pyrroline-5-carboxylate reductase (P-5-CR) and γ -glutamyl kinase which are the enzymes related to Pro anabolism. But, in contrast, it reduced the activity of Pro oxidase [61]. In the case of pretreatment with SA, it also showed some positive results. *Solanum lycopersicum* seeds pretreated with 10 μM SA improved the chl content and reduced MDA content under salt stress (100 mM NaCl) [38]. Higher accumulation of abscisic acid (ABA) in shoot and enhancement of water potential of SA-treated seedlings compared to the seedlings exposed to salt alone were also observed [38]. These results were supported by Horváth et al. [62] in the same plants with the equal concentrations of SA. Similarly, when pretreatment with SA (0.5 and 1.0 mM) was done, *Gerbera jamesonii* seedlings also showed positive results in salt stress (100 mM). Salicylic acid application reduced the EL, MDA and Pro contents and increased the activities of SOD, catalase (CAT), peroxidase (POD), and APX compared to salt stressed seedlings [39]. But, these effects were more acceptable in case of lower (0.5 mM) concentration of SA. Recently, Nazar et al. [41] again used SA (0.5 mM) to demonstrate the preventive role of it in *Brassica juncea* seedlings exposed to 100 mM of NaCl stress for 30 consecutive days. Application of SA reduced thiobarbituric acid reactive substances (TBARS) and H_2O_2 contents, also dehydroascorbate (DHA) and GSSG contents. It was found to increase the activities of dehydroascorbate reductase (DHAR), APX, and GR to a remarkable content. And most importantly, it reduced the toxic Na^+ and Cl^- uptake to almost half of the salt-stressed plants [41].

From the above-mentioned studies, the role of SA in alleviating salt stress can be considered as clear and concise. But, there are also some points to be considered as higher concentrations of SA may itself cause damage to plants [12, 59] and very lower concentrations may have a minimum effect [42, 62] against salt stress. So, the concentration of SA, application method and time, duration of salt stress and plant age are some of the important points to be considered while using SA against salt stress.

3.2. Drought

Drought stress is one of the most devastating abiotic stresses adversely affecting growth and developmental processes of the plant. Drought stress affects the physiological processes, brings biochemical changes, leads to the formation of secondary metabolites, significantly accumulates endogenous reactive oxygen species (ROS) and increases toxins (such as methylglyoxal). Drought stress hampering the reproductive development drastically reduces yield or productivity of plants [67].

Several studies demonstrated and proved the pivotal roles of SA in alleviating drought damage and improving drought stress tolerance in plants (**Table 2**). Salicylic acid pretreatment (0.5 mM) alleviated substantial water loss and its damaging effects on wheat seedlings that enhanced drought tolerance [43]. Pretreatment with SA upregulated 37 protein spots under drought stress which has been investigated through proteomics. Glutathione S-transferases, APX, and 2-cysteine peroxiredoxin were enhanced under drought stress. Enhancement of antioxidant defense system worked against the oxidative damage [43]. Proteins involved in ATP synthesis are also upregulated by SA under drought stress. Salicylic acid supplementation with drought also upregulated 21 protein spots, including RuBisCo and related enzymes [43]. In their other experiment, influential role of SA was also demonstrated on AsA-GSH cycle [68]. Exogenous SA supplementation enhanced the transcription of *GST1*, *GST2*, *GR*, and *MDHAR* genes during almost the entire drought period. The increase of *DHAR* was noticed at 12 h, *GPX1* at 48 h, phospholipid hydroperoxide glutathione peroxidase (*GPX2*) at 12 and 24 h, and glutathione synthetase (*GSHS*) at 12, 24, and 48 h of drought stress. Upregulation of transcription level of AsA-GSH cycle enzymes contributed to drought tolerance [68]. SA-accumulating (*siz1* and *cpr5*) genes were highly expressed in guard cells of drought which modulated movement of stomatal aperture in *Arabidopsis* plants. The generation of ROS was also modulated in this plant [69]. In tomato (*Lycopersicon esculentum*), SA treatment with drought has been demonstrated to protect the activity of nitrate reductase which helps to maintain the protein and nitrogen contents of the leaves, compared to the drought affected plant without SA addition. Photosynthetic parameters, membrane stability, water potential and activity of carbonic anhydrase were maintained by SA which also contributed to drought stress tolerance [70]. In sunflower, water stress-induced decrease in the yield and oil content. Salicylic acid (0.724 mM) application increased the Pro content, head diameter, number of achene, 1000-achene weight, achene yield, and oil yield of sunflower, compared to drought treatment alone [71]. The addition of acetyl SA in (0.1–1.0 mM) also improved drought tolerance of muskmelon seedlings [72]. Two wheat varieties viz. Wafaq-2001 and Punjab-96 were subjected to drought stress. Drought stress significantly decreased membrane stability index (MSI) and yield. Salicylic acid supplementation caused 37% increase in soluble sugars in Wafaq-2001 cultivar which was higher, compared to Punjab-96 cultivar. Salicylic acid also increased protein content and MSI in both cultivars with a higher increase in Wafaq-2001. The overall drought tolerance was higher in Wafaq-2001 after SA application which is evident from higher yield [73]. Exogenous addition of SA increased the activity of antioxidant enzymes which helped to alleviate the drought stress damage in *Ctenanthe setosa* [74]. Mustard (*B. juncea* L. cv. BARI Sharisha 11) seedlings were subjected to two different levels of drought with 10 and 20% polyethylene glycol (PEG) for 48 h. Leaf relative water content (RWC), chl *b* and chl (*a + b*) decreased but Pro content increased. Disrupting the antioxidant defense system, drought stress increased oxidative damage which was indicated by high MDA and H₂O₂ levels. Supplementation of SA in drought-stressed seedlings increased the leaf RWC and chl content, increased the AsA and GSH, decreased the GSSG content, and maintained a higher ratio of GSH/GSSG. Salicylic acid increased the activities of monodehydroascorbate reductase (MDHAR), DHAR, GR, glutathione peroxidase (GPX), CAT, glyoxalase I (Gly I), and glyoxalase II (Gly II) in drought affected seedlings as compared to the drought-stressed plants without SA supplementation, with a concomitant decrease in H₂O₂ and lipid peroxidation

level [44]. Methyl-SA (at 0.1 mM) spray promoted drought-induced leaf senescence in *Salvia officinalis* [75]. Drought stress adversely affected growth performance of winter wheat, Cheyenne. Application of SA analogue 4-hydroxybenzoic acid (4-HBA) increased drought tolerance of winter wheat Cheyenne [16]. Foliar application of SA (10 μ M) protects lemongrass (*Cymbopogon flexuosus* Steud. Wats.) varieties (Neema and Krishna) from drought stress by improving growth parameters, modulating the activities of nitrate reductase, carbonic anhydrase, and EL, Pro content, free amino acid, and in PEP carboxylase activity [76].

3.3. Extreme temperatures

Temperature is one of the vital factors that determine plants establishment, growth, development, and productivity. Due to climate change, global average temperature is fluctuating very rapidly and threatening the survival of living beings. Thus, among the various abiotic stresses, extreme temperature has become the talk of the topic in recent decades because of its devastating and damaging effects on plants [84]. Extreme temperature includes both high temperature (HT) and low temperature (LT) that can injure plants. The high temperature is the increasing of temperature beyond the critical threshold level that can deplete plant growth and metabolism depending on the sufficient time period [85]. Heat stress often becomes worse because of its combination with other stresses including drought [86]. High temperature severely alters the plant physiological processes including germination, photosynthesis, respiration, transpiration, partitioning of dry matter, etc. [87]. In addition, HT results in enzyme inactivation, protein denaturation, disruption of proteins and membranes which ultimately affects plant growth [88, 89]. Low-temperature consists of both freezing ($<0^{\circ}\text{C}$) and chilling ($0\text{--}15^{\circ}\text{C}$) temperatures. In chilling stress plant faces injury without formation of ice whereas, in freezing stress, the formation of ice occurs in plant tissues. Chilling and freezing stresses are together called cold stress or LT stress. Low-temperature stress shows various damaging symptoms in plants including faster senescence and decay [90, 91], interference with germination, cell membrane disruption, photosynthesis, water and nutrients uptake, reproductive development as well as growth and yield [92]. Either HT or LT conditions, at molecular level, leads to the overproduction of ROS which ultimately gives rise to the oxidative stress [84, 93]. Nowadays, to develop temperature-stress tolerance, the use of exogenous SA is one of the common approaches. Salicylic acid being the endogenous growth regulator or phytohormone acts as an important signaling molecule and develops abiotic stress tolerance in plants [94]. Recent advances on SA-mediated temperature stress tolerance have been listed in **Table 3**.

High temperature (30°C) resulted in a significant reduction in FW and soluble starch synthase activity of *T. aestivum* [46]. Foliar application of SA improved the FW, total RNA, and soluble starch synthase activity. In *Z. mays*, HT ($40 \pm 1^{\circ}\text{C}$) induced oxidative damage and reductions in dry biomass were reversed by exogenous SA treatment. SA developed HT tolerance by improving CAT, SOD, and POX activities [48]. The effects of SA on seed germination and physiological attributes of heat stressed ($32/26^{\circ}\text{C}$, 12/12 h, day/night) *L. lycopersicum* were investigated. It has been revealed that SA reduced the germination time and increased the germination percentage together with the increased vitamin, lycopene, total soluble solid (TSS) and titratable acidity (TA) contents [49]. Temperature above 40°C , increased TBARS and H_2O_2 contents but decreased the net photosynthesis, RuBisCo activity, chl, and WUE of *T. aestivum*

plant. Negative HT effects were counteracted significantly by exogenous SA supplementation [13]. Heat stress (45°C) in *Digitalis trojana Ioanina*, compared to its normal temperature, lowered the important antioxidant enzymes (CAT and SOD) activities. Pretreatment with SA significantly increased CAT and SOD activities with increased Pro, phenolic, and flavonoid contents [47]. The sharp decline of photosynthetic apparatus was found in *Vitis vinifera* in response to heat (43°C) stress. Alleviation of photosynthetic rate and RuBisCo activity were found when pretreated with SA [95]. *Cannabis sativa* induced thermotolerance against (40°C) temperature, when supplied with exogenous SA, were studied. Improved activities of antioxidant enzymes (SOD, DHAR, GPX, APX, and GR) were documented with decreased CAT activity. Decreased EL percentage with reduced H₂O₂ and TBARS contents were also evident [97]. Salicylic acid involved in various protective functions in *B. juncea* after HT (30 or 40°C) exposure. However, increased growth, g_s and CO₂ fixation along with improved defense system were found with SA treatment [98]. Chilling (5°C) stressed *Musa acuminata* when treated with exogenous SA increased SOD, CAT, and APX activities with decreased H₂O₂ accumulation [99]. Low temperature (3°C) disrupted the RuBPC and PEPC activities with decreased rate of CO₂ assimilation and respiration. Treatment with SA improved the activity and ameliorated the chilling effects [100]. Performance of *V. vinifera* was investigated upon HT (38 – 0.5°C) [101]. Pretreatment with SA increased H⁺ and Ca²⁺-ATPase activities with cerium phosphate grain appearance and thus gave higher stress tolerance. Wang and Li [102] noted that upon freezing (–3°C) stress in *V. vinifera*, besides upregulating antioxidants, increased maintenance of AsA-GSH pool and cytosolic Ca²⁺ homeostasis caused improved heat stress tolerance. High-temperature stress mediated increased ROS generation and oxidative stresses have been reported in several other plant species. Exogenous SA treatment resulted in the reduced ROS generation and oxidative stress in *Pratylenchus pratensis* [103], *Arabidopsis thaliana* [109]. Night ambient temperature ranges from 27 to 32°C in *Oryza sativa* caused the significant reduction in spikelet fertility and grain size. Exogenous SA treatment improved the rice grain fertility and hence, increased yield [104]. *Prunus persica* fruits were pretreated with SA before imposition of chilling injury (0°C). Reduced chilling injury was observed due to higher activities of antioxidants and heat shock protein 101 (HSP101) expression [105]. Leaves of heat (38/30°C, day/night) stressed *Rhododendron* became withered, defoliated, and brown. Total soluble protein and Chl contents were also reduced. Lower damage rate of leaves with higher chl and soluble protein were observed when supplemented with SA [106]. In a study with HT stressed (50°C) *V. radiata*, SA treatment increased the CAT, APX, POD, and GSH contents with enhanced defense system and radical scavenging mechanism [107].

3.4. Toxic metal/metalloids

In the industrial era, the most important and potential threat for crop production is the abiotic stress. Among them, toxic metal stress is one of the major concerns. Growing population and fast industrialization coincide together, results in the generation and dissemination of huge amount of toxic metals in the environment [110]. Toxic metal consists of a set of harmful elements having no biological role in organisms such as Cd, Pb, Hg, St, Al, etc. Although toxic metals and heavy metals (HMs) are often thought to be synonymous, some lighter metals such as Al may also cause toxicity. Toxic and HMs are differed in the case of their biological role.

Some HMs having a biological role in plants also considered toxic when they are used in high concentrations, viz. Ni, Cu, Zn, etc. On the other hand, metalloids include those elements that show behavior both like metals and nonmetals including B, Si, Ge, Sn, As, Sb, etc. The underlying parent material and atmosphere are the two main sources of toxic metals. Metals are uptaken and accumulated easily by plants and causes toxicity within the plant tissue. They directly interact with the proteins, enzymes, and causes phytotoxicity. The inhibition of growth rate is the most certain consequences of metal toxicity [111]. Leaf rolling, chlorosis, necrosis, stunted growth, stomatal dysfunctioning, cation efflux, reduced water potential, alterations in the membrane, photosynthesis, metabolism, and various key enzymes are some other toxic metal effects in plants [111, 112]. Toxic metals also manipulate the nutrient homeostasis, water uptake, transport, transpiration, respiration, and ultimately may lead to plant death [113, 114]. Metal toxicity at the cellular level results in the overproduction of ROS [110]. To mitigate metal induced stresses in plants, plant biologists are trying to develop new strategies. Salicylic acid is a very important molecule that induces defense responses against various toxic metal/metalloids stresses (**Table 4**).

Several research findings demonstrated that exogenously applied SA improved the growth and photosynthetic traits in different plants by reducing the damaging effects of toxic metals. *O. sativa* exposed to As (25 and 50 μM) [50], *A. thaliana* exposed to As (100 μM) [115], *T. aestivum* exposed to Cd (500 and 1000 μM) [121], and *Z. mays* exposed to Cr (500 ppm) [52] grown well under SA supplementation. In a recent study, SA pretreatment reduced the oxidative stress in *T. aestivum* after Cd (0.01, 0.1, and 1 mM) exposure. Cd stress increased the lipid peroxidation and EL percentage. But the exogenous application of SA significantly declined the MDA content and EL percentage [53]. Salicylic acid also evidenced to alleviate the oxidative stress induced by metal toxicity in several other plant species by decreasing the toxic effects of overproduced ROS and lipid peroxidation. In *O. sativa*, enhanced MDA and H_2O_2 contents induced by As (25 and 50 μM) were reduced by the exogenous SA pretreatment [50]. Similarly, adverse oxidative stress was also demonstrated in *Lolium perenne* as induced by Cd (100 μM). Results showed that increased accumulation of $\text{O}_2^{\bullet-}$, H_2O_2 , and higher MDA were decreased by SA application. Some other research findings also supported that the SA mitigates metal-induced oxidative damage in *Pisum sativum* [136], *Brassica oleracea* var. botrytis [135], *Medicago sativa* [134], etc. It was reported that treatment with SA alleviated the Cd (15 μM) induced root growth inhibition and improved the antioxidant activities thus reduced the Cd-induced oxidative stress in *Hordeum vulgare* [51]. Salicylic acid supplementation in As (100 μM) stressed *A. thaliana* showed improved performance in terms of antioxidant enzymes (APX, CAT, SOD) activities and enhanced tolerance to metal stress. In other experiment it was demonstrated that when SA was exogenously applied against Cd (0.25, or 0.50 mM) stress, increased amelioration of metal stress was observed with increasing activities of defense responsive genes and upregulating the antioxidant (SOD, CAT, APX, and GR) enzymes [117]. Decreased root growth, RWC, and increased oxidative stress were decreased by seed priming with SA [118]. Under Cd (50 and 100 mM) stress, plant growth, chl, total lipid contents, and nutrient absorption became decreased which were further increased by soaking seeds with SA. Increased stress tolerance with reduction of oxidative damage was also evident [119]. Increased ROS production, TBARS content, and EL with increased SOD, CAT, and APX activities were found after Cd (50 and 100 μM) exposure.

Seed priming with SA significantly decreased the oxidative damage and increased the antioxidant enzymes activities. Agami and Mohamed [121] reported that SA efficiently alleviated the adverse Cd (500 and 1000 μM) stress by restoring the growth parameters and increasing the antioxidant defense system. Exogenous SA developed Cr (mg L^{-1}) stress tolerance by improving growth, photosynthetic pigments and oxidative stress reduction by upregulating antioxidant defense system [52]. Inhibited antioxidant enzymes (APX, CAT, POX, and SOD), soluble sugars and chl contents were showed when *T. aestivum* exposed to Pb (10, 50, 100, 200 mg L^{-1}). Alleviated inhibitory effects were found after SA supplementation as cotreatment [126]. In *Zygophyllum fabago*, increased Pb accumulation after Pb (0.75 mM) exposure was reduced by SA pretreatment. Upregulated antioxidants and downregulated oxidative damage together induced stress tolerance [125]. Salicylic acid treatment against Cd (5, 10 or 50 mM) stress increased tolerance in *P. pratensis* by controlling uncontrolled absorption of Cd and maintaining nutrients (K, Ca, Fe, Mg) homeostasis [127]. Effects of B was investigated (25 and 50 mg kg^{-1}) toxicity in *Daucus carota* and *S. oleracea*. In both plants, the growth, physiology, and antioxidant enzymes activity were affected by B toxicity. But exogenous SA application showed some protective effects in the alleviation of the metal toxicity [128, 129]. A similar finding was also demonstrated by Shi and Zhu [131] in *Crocus sativus* plant. Exposure to a toxic level of Mn (600 μM) with SA in *C. sativus* plant, maintained nutrient (Ca, Mg, Zn) homeostasis, reduced metal stress, and improved tolerance. Recent findings in *B. juncea* against Mn (3, 6, or 9 mM) toxicity revealed that SA is an important regulator of photosynthetic enzymes including carbonic anhydrase (CA). It together with the upregulated defense system and reduced oxidative damage-regulated the photosynthesis in a concentration-dependent manner [130]. Besides upregulation of antioxidant enzymes, SA involved in the activation of CaM-like protein genes and cytosolic Ca^{2+} in Al (30 μM) stressed *Glycine max*. It has been showed that increased metal stress tolerance resulted from exogenous SA treatment [132]. Effect of exogenous SA was investigated upon Pb (50 μM) stressed *Vallisneria natans*. Decreased chl, carotenoid, NADPH oxidase, nonprotein thiols, AsA but increased CAT, DHAR, and POD activities were observed. Pretreatment with SA increased the activities of NADH oxidase, AsA, and GSH in Hg (10 μM) stressed *M. sativa* and thus developed better tolerance to stress [133]. Recent evidences suggested that SA develops stress tolerance by involving in the regulation of photosynthetic pigments, activities of CA, NR, and anticancer alkaloids (vincristine and vinblastine) upon Ni (50, 100, and 150 mg kg^{-1}) exposure in *Catharanth roseus* [122]. Toxic level of Ni (0.5 mM) impacts on *Brassicca napus* also suggested that application of SA decreased the leaves' toxicity symptoms (chlorosis, necrosis, etc.) and improved growth and survival [123]. Recently a combined effect of metals (Co, Ni, Cd, Cr, and Pb) (0.25 M) on *B. oleracea* var. botrytis has been investigated. It has been found that SA alleviated all the toxic effects of metals except for Cr. In the case of Cr, SA accelerated the toxic effects and the plant died [135]. Improved CO_2 fixation, RuBPC activity, and chl content were found in Cd (0.5, 1, 2, and 5 μM) stressed *P. sativum* when supplied with exogenous SA.

3.5. Ozone and ultraviolet radiation

Due to the gradual increase in atmospheric ozone (O_3) concentration, it has become a major threat for plant species mainly because of its pollutant and photochemical oxidant affects [139]. Significant crop losses due to O_3 damage is predicted to be increased by 25% in background O_3

concentration over the next 30–50 years [140]. High concentrations of ozone induce oxidative stress, which activates programmed cell death and significantly inhibits plant growth, causing plant death and loss of quality [141]. It is the most noteworthy atmospheric pollutant in terms of phytotoxicity. It is to be noted that in the concentration of O₃ has been decreased by 5% in the past 50 years due to the release of anthropogenic pollutants and, a larger proportion of the UV radiation (especially (UV-B) spectrum reaches the Earth's surface [142]. Although sunlight plays an integral role in harvesting light energy through photosynthesis, high light, especially ultraviolet (UV) radiation, resulted in stress to plants, which include damage to DNA, proteins, and other cellular components [143]. This episode is unavoidable as 7% of the electromagnetic radiation emitted from the sun is in the UV range (200–400 nm). UV radiation also leads to oxidative stress by photooxidation and excess generation of ROS [84]. To cope up the adverse effects of both O₃ and UV radiation needs some adaptive mechanisms. In few plant species, SA was found to take part in enhancing the tolerance to O₃ and UV radiation mainly by enhancing antioxidant defense and improving plant growth.

In *A. thaliana*, UV-C light stress activated the transition to flowering through SA. SA could regulate the time of flowering by inducing photoperiod and autonomous pathways which are evident by late flowering in SA-deficient plants. While investigating the genes responsible for flowering induction viz. *constans* (*CO*), *flowering locus T* (*FT*), *suppressor of overexpression of constans 1* (*SOC1*), and *flowering locus C* (*FLC*) it was observed that the expression of *CO*, *FT*, and *SOC1* transcripts decreased to around 50% in long day-grown SA-deficient plants when compared to control plants [54]. In short day plants, only the levels of *FT* transcripts were reduced compared to *CO*. Thus, it indicated that SA might play important role in flowering under UV radiation [54]. The effect of UV was investigated (UV-A: 320–390 nm, UV-B: 312 nm, and UV-C: 254 nm radiation with a density of 6.1, 5.8, and 5.7 W m⁻²) on *Capsicum annuum* plants and found that activities of antioxidant enzymes were enhanced in leaves in response to UV-B and UV-C radiation. Moreover, SA treatment showed further enhancement in the activities of POD, APX, CAT, and GR while some other enzymes were modulated [55]. In another report, a clear decline was reported in photosynthetic pigments (chl *a*, chl *b*, and carotenoid) under UV-A, UV-B, and UV-C, while a foliar spray of SA recovered this decline. The level of anthocyanins, flavonoids, and rutin in SA-treated plants was also higher than in a UV-exposed plant grown without SA [56]. *V. radiata*, exposed to UV-B radiation (ambient+4–8 kJ m⁻²) showed declined growth, photosynthetic pigments and photosynthesis (F_v/F_m and qP except NPQ) which were accompanied by significant decrease in SA level [57]. UV radiation also causes overproduction of ROS and concomitantly damaging effects on lipids, proteins, and membrane stability. However, SA pretreatment significantly alleviated the adverse effects. They also revealed that UV-B altered SA biosynthesis and SA-pretreatment might act as a signal that reduces oxidative stress by triggering upregulation of antioxidant defense and subsequent improvement of growth and photosynthesis [57]. In *Satureja hortensis*, both UV-B and UV-C exhibited decreased plant growth (plant height, root length, shoot DW, and leaf area), node number, internode distance and chl content, while stem diameter, leaf thickness, flavonoid content, phenolic content, and antioxidant activity were increased [58]. The increase in secondary metabolite such as flavonoid content, phenolics might be able to protect cells against free radicals but this level was not well enough under severe stress. On the other hand,

plants treated with 1 mM SA exhibited higher growth and improved physiology compared to nontreated one and subsequently showed better appearance under UV radiation [58].

4. Salicylic acid and ROS detoxification

Salicylic acid is the most studied phytohormone regarding its role in oxidative stress. Due to its multifarious actions, it has been found very effective in detoxifying ROS in plant cells (**Figure 2**). According to Janda and Ruelland [144], SA-induced tolerance to abiotic stresses such as chilling, heat, heavy metals, osmotic stress, and salinity is involved in activation of the stress-induced antioxidant system. It has been demonstrated that SA could significantly improve both photosynthesis parameters and antioxidant defense system in conferring salt stress tolerance in *V. radiata* [17]. In *O. sativa*, exogenous SA significantly reduced the oxidative burst by reducing H_2O_2 and $\text{O}_2^{\bullet-}$ contents under herbicide exposure which was mainly due to the SA-mediated upregulation of antioxidant defense enzymes (SOD, POD, CAT, APX, GR, and GST) and efficient GSH pool. The positive role of SA is mostly dependent on their dose and application methods [145]. Other study also proved that SA-mediated antioxidative defense system was dependent on the concentration used and the method of application [146]. In *T. aestivum*, 0.25 mM SA resulted in marked increase in the antioxidant enzyme activities (SOD, CAT, POD, GPX, APX, and GR), while the treatment with 2.5 mM SA resulted in a decrease in the activities under water stress [146]. A lower dose of SA also maintains higher AsA pool which in turns significantly scavenged the ROS. This ROS detoxification induced by SA also associated with improved photosystem II (PSII) efficiency. Belkadhi et al. [147] showed that *Linum usitatissimum* plants showed a lower amount of lipid and protein oxidation and membrane oxidation under Cd stress when pretreated with SA. This protection was availed by the enhanced activities of SOD, GPX, and APX as well as the 2,2'-diphenyl-1-picrylhydrazyl (DPPH) scavenging activity and ferric-reducing antioxidant power (FRAP). Increases in MDHAR, DHAR, GR, GPX, and CAT activities 53, 64, 49, 82, and 65% were noticed in PEG-treated *B. juncea* seedlings when sprayed with 50 μM SA [44]. SA-induced upregulation of antioxidant enzymes caused 32 and 26% decrease in MDA and H_2O_2 content compared to drought (20% PEG, 48 h) alone. One of our research results showed that exogenous SA enhanced the activities of antioxidant enzymes and nonenzymatic antioxidants under salt stress (200 mM NaCl, 48 h). Compared to salt stress alone, NaCl + SA resulted in 41, 107, 25, 37, 44, and 59% increases in MDHAR, DHAR, GR, GST, GPX, and CAT activities [40]. Salicylic acid supplementation also increased AsA and GSH content by 48 and 39%, respectively and enhanced GSH/GSSG ratio by 47% compared to salt stress alone. As a result, MDA and H_2O_2 contents decreased by 39 and 31% [40]. In *Nitraria tangutorum* SA mitigated salt-induced oxidative stress (evidenced by a marked reduction in MDA and H_2O_2 content) by upregulating the activities of SOD, POD, and CAT. The content of MDA in the 1.5 mM SA treated seedlings under 100–400 mM NaCl treatments declined to 2.27–3.59 fold of the control which was a clear sign of the reduction of oxidative stress [148]. However, some of the enzymes like APX activity was inhibited at higher concentrations (1.0 and 1.5 mM) of SAMDA content was measured with 1.5 mM SA applied, and the contents of MDA in the leaves of SA-treated seedlings under 100–400 mM NaCl treatments declined to only 2.27–3.59 fold of the control.

5. Interaction of SA with other signaling molecules

Salicylic acid not only exerts its positive effect independently but also interacts with other signaling molecules, phytohormones, and other phytoprotectants. These interactions show different signaling events and ultimate protection to plants from stress-induced damages (**Figure 3**). In grapevines, Wang and Li [102] showed improved Ca^{2+} homeostasis and associated antioxidant defenses under heat and cold stress-regulated by SA. When plants were treated with exogenous SA, they showed enhanced PM- Ca^{2+} ATPases and V- Ca^{2+} ATPases activities. Moreover, Ca^{2+} precipitates were shown on the inner side of the plasma membrane, and less were in intercellular spaces and the vacuole. However, in SA treated plants Ca^{2+} precipitates were in vacuoles, and few were on the inner side of the plasma membrane. Ca^{2+} precipitates in chloroplasts were bigger even after heat or cold stress. Importantly, SA treatment caused enhancement of the activities of APX, GR, and MDHAR, which efficiently reduced the lipid peroxidation and relative EL (REL), which concluded that exogenous SA could mitigate oxidative stress by maintaining Ca^{2+} homeostasis under extreme temperature stress [102]. In *O. sativa*, Wang et al. [145] reported that SA treatment downregulated ABA genes more in cultivar XS 134, which correlated with the enhanced tolerance to quinclorac-induced oxidative stress. Application of SA had obvious effects on all of the ABA-related genes and inhibited the expression of *OsABA8ox1*, *OsABA8ox2*, *OsABA8ox3*, *OsNCED1*, *OsNCED2*, and *OsNCED3* as compared to quinclorac stress alone. Since overproduction of ABA and ROS is highly associated this downregulation protected the plants from herbicide-induced damages. Wang et al. [145] also reported SA-induced inhibition of ABA synthesizing enzymes. Leslie and Romani [149] reported that SA inhibited ethylene formation which triggered biosynthesis of ABA under stress conditions [150]. In the adventitious roots of *Panax ginseng*, SA-induced enhancement of the activities of NADPH oxidase, SOD, CAT, POD, and APX was evident while no significant effect on AsA and GSH content were observed [151]. These effects were mostly NO-dependent and it was also observed that SA-induced the generation of NO. They revealed that at lower concentration (100 μM) SA was highly effective in inducing the

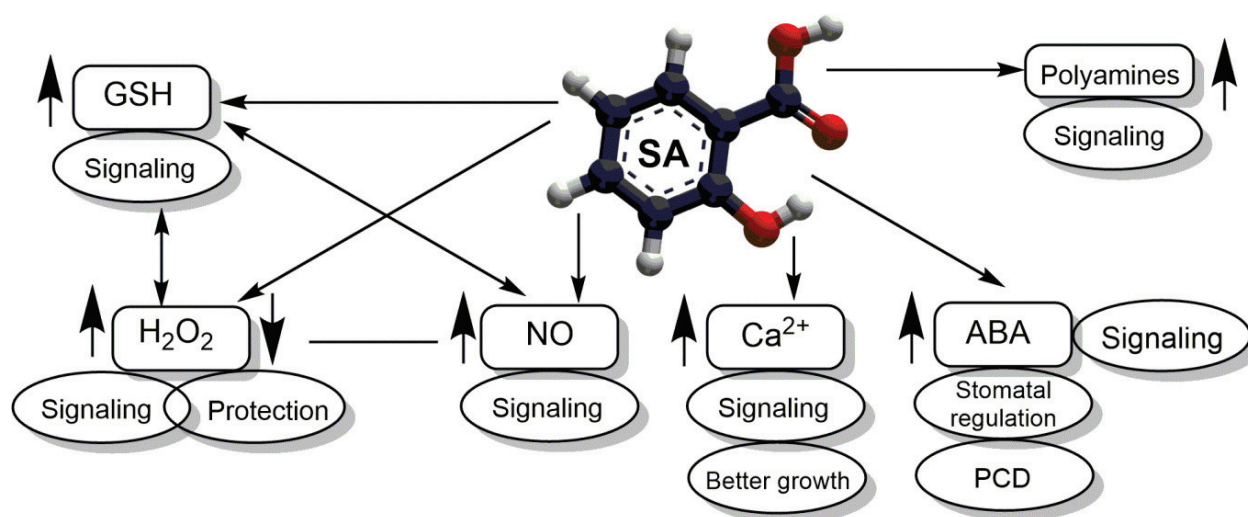


Figure 3. Interaction of SA with other signaling molecules to elicit defense responses in plants.

accumulation of NO, $O_2^{\bullet-}$ and it took part in stress signaling. Interactive effects of SA and NO were studied in mitigating osmotic stress (-0.4 MPa) in *T. aestivum*. It was observed that osmotic stress induced chl degradation and membrane instability, and H_2O_2 generation and lipid peroxidation were effectively reduced by exogenous application of SA or SNP, which was associated with the enhancement of antioxidant defense. However, pretreatment of plants with methylene blue (MB; as a guanylate cyclase inhibitor) reversed or reduced the protective effects of SA and SNP suggesting that the protective effects were likely attributed to NO signaling. They also concluded that NO may act as downstream of SA signaling in the reduction of induced oxidative damage [152]. SA-mediated H_2O_2 signaling and subsequent Cd stress tolerance was revealed in *L. usitatissimum* [147]. Seedlings pretreated with 250 or 1000 μ M SA resulted in enhanced production of H_2O_2 because of inhibited CAT activity. Although the control plants with SA pretreatment showed significant (1.2 fold) increase in H_2O_2 , this level is remarkably lower when compared with Cd alone and Cd+SA. These results indicated that SA could regulate the Cd-induced oxidative stress because Cd-treated seedlings primed with SA exhibited a higher level of total antioxidant capacities and increased activities of H_2O_2 -detoxifying enzymes [147]. Exogenous SA application was found to activate GSH synthesis in *B. juncea* and *B. napus* and showed enhanced protection against drought- and salt-induced oxidative damages [44, 40].

6. Conclusions and perspectives

Salicylic acid plays an important role in the regulation of growth and physiology in relation to the abiotic stress responses of plants. The SA was found to be effective in the different form of application foliar spray/incorporation with growing media depending upon plant species. The low concentration of SA showed advantageous effects in abiotic stress tolerance of plants. In contrast, the high concentration of SA showed toxic effects. Thus, both the concentration and application method of SA are critical to obtaining its best effect on different plant species. In the biosynthesis pathway of SA, there are unknown steps and enzymes which should be discovered. The catabolism and the further fate of transformed product of SA are not known clearly. How SA interacts and being regulated by the cross-talk in harmony with other phytohormones and plant growth regulators working (auxins, cytokinins, gibberellins, ethylene, jasmonates, brassinosteroids, etc.) and other signaling molecules (NO, H_2O_2) were not studied extensively. SA-mediated defense networks and insights into the cross-talk of SA with other defense-signaling pathways should be revealed. An integrated approach combining the knowledge of genetics, molecular biology, biochemistry, genomics, and bioinformatics techniques is a useful tool to study the functioning of SA in plants. Clear understanding of the biosynthesis and catabolic pathway and other unanswered question are vital to exploit SA as a potent phytoprotectant molecule to improve abiotic stress tolerances.

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Author contributions

M.H. performed literature reviews and drafted the manuscript; K.N., T.I.A. and T.F.B., M.I. and M.H. contributed the review for literature research; M.F. and H.O. reviewed the manuscript and approved the final draft.

Conflicts of interest

The authors declare no conflict of interest.

Abbreviations

4-HBA	4-hydroxybenzoic acid
ABA	Abscisic acid
APX	Ascorbate peroxidase
AsA	Ascorbate/ascorbic acid
BA2H	Benzoic acid-2-hydroxylase
CAT	Catalase
chl	Chlorophyll
C _i	Intercellular CO ₂ concentration
DAS	Days after sowing
DHA	Dehydroascorbate
DHAR	Dehydroascorbate reductase
DPPH	2,2'-diphenyl-1-picrylhydrazyl
DW	Dry weight
EL	Electrolyte leakage
FRAP	Ferric reducing antioxidant power
FW	Fresh weight
GB	Glycinebetaine
Gly I	Glyoxalase I
Gly II	Glyoxalase II
GO	Glycolate oxidase
GR	Glutathione reductase
g _s	Substomatal conductance
GSH	Reduced glutathione
GSSG	Oxidized glutathione
GST	Glutathione S-transferase

HSPs	Heat shock proteins
HT	High temperature
IC	Isochorismate
ICS	Isochorismate synthase
IPL	Isochorismate pyruvate lyase
LOX	Lipoxygenase
LT	Low temperature
MAPK	Mitogen-activated protein kinase
MB	Methylene blue
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
MeSA	Methyl salicylate
MSI	Membrane stability index
NADH	Nicotinamide adenine dinucleotide phosphate
NO	Nitric oxide
PAL	Phenylalanine ammonia-lyase
PEG	Polyethylene glycol
P_n	Net photosynthesis
POD	Peroxidase
POX	Peroxidases
Pro	Proline
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicylic acid
SA-Asp	Salicyloyl-L-aspartic acid
SAG	Salicylic acid 2-O- β -glucoside
SAT	Serine acetyl transferase
SGE	Salicyloyl glucose ester
SNP	Sodium nitroprusside
SOD	Superoxide dismutase
TBARS	Thiobarbituric acid reactive substances
T_r	Transpiration rate
TSS	Total soluble solid
WUE	Water use efficiency

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