

Salicylic Acid Combats Abiotic Stresses in Plants

Subjects: Plant Sciences

Contributor: Junli Liu, Gaoyang Qiu, Chen Liu, Hua Li, Xiaodong Chen, Qinglin Fu, Yicheng Lin, Bin Guo

Salicylic acid (SA) is a plant hormone that has been implicated in processes not limited to plant growth, development, and responses to environmental stress. The various roles and functions of SA in mitigating abiotic stresses to plants, including heating, chilling, salinity, metal toxicity, drought, ultraviolet radiation, etc were summarized. Consistent with its critical roles in plant abiotic tolerance, the gaps in the literature with regard to the complex signalling network between SA and reactive oxygen species, ABA, Ca^{2+} , and nitric oxide were identified. Furthermore, the molecular mechanisms underlying signalling networks that control development and stress responses in plants, and underscore prospects for future research on SA concerning abiotic-stressed plants were also discussed.

Keywords: abiotic stress ; reactive oxygen species ; salicylic acid

1. Functions of SA in Mitigating Abiotic Stresses

1.1. Heat

Global warming is causing a serious threat to plant growth and food security. Heat stress disturbs plant cellular homeostasis, retards development, and causes sterility and reduced yield [1]. It has been reported that the application of exogenous SA enhances rice yield under high-temperature conditions [2], while inhibiting the synthesis of SA markedly reduced the level of thermotolerance in pea plants [3]. Furthermore, the biosynthesis of SA was increased under heat stress, as observed in many plant species, such as mustard [4], creeping bentgrass [5], grape [6], and melon [7].

Photosystem II, which functions as an electron transport chain in chloroplasts, is one of the most thermosensitive structures in plants [8]. A study found that spraying 0.25 mM SA onto alfalfa leaves for 5 days ameliorated the heat damage to PSII and photosynthetic efficiency [9]. This may be because SA improves the antioxidant system and chlorophyll fluorescence [10], thus maintaining the thermo-stability of the electron donor and reaction centres of PSII [11]. Heat stress also disturbs osmotic potential and destroys plasma membranes, thereby leading to ion leakage in plant cells. The application of SA can enhance free proline content, which plays a key role in the osmoregulation of plant cells. This phenomenon has been widely observed in wheat [12], cucumber [10], and tomato [13][14]. Furthermore, spraying 100 mM SA on grape leaves stabilized the activity of the proton pumps in membranes, including H^{+} - and Ca^{2+} -ATPase, which may be another important mechanism for maintaining the integrity of the membrane under heat stress [15]. Activities of SA contribute to better regulation of stomatal aperture along with photosynthetic apparatus, such as PSII and Rubisco activity, and thus increase the capacity of photosynthesis when subjected to stressful temperature conditions [14].

Transcriptome analysis of plants has revealed SA signalling of heat-stress-responsive genes during thermotolerance, such as NPR1 (non-expressor of pathogenesis-related), HSPs (heat shock proteins), MBF1c (multiprotein bridging factor 1c), TGA, and PR-1 (pathogenesis-related protein 1) [5][16]. Exogenous application of SA induces the synthesis of heat shock proteins (HSPs), the proteins chiefly responsible for defence against heat stress, as noted in *Arabidopsis thaliana* plants [17], tomato [18][19], and rice [20]. However, a study with transgenic *Arabidopsis* obtained the inconsistent results that SA failed to affect the expression of Hsp [17], indicating the molecular mechanism still needs to be further investigated. Endogenous free SA stimulated the production of PIP2-phospholipase C of pea, a lipid-associated enzyme involved in intracellular signalling, in response to heat treatment. In response to heat stress, the pea plant elevated the synthesis of SA initially, which then signalled the production of PIP2-phospholipase C, a lipid-associated enzyme involved in intracellular signalling [21]. SA also increases the expression of the chitinase-1 gene in melons under heat shock [7]. Furthermore, cross-talk between SA and other plant signalling, such as H_2S , Ca^{2+} , IAA, and ABA, has also been reported [22][23][24]. For example, treatment with SA increases the activity of L-cysteine desulphydrase, a key enzyme in H_2S biosynthesis, indicating that H_2S might be a downstream signalling molecule in SA-induced heat tolerance [22].

1.2. Chilling

Chilling injury is one of the main limitations in the growth and productivity of tropical and subtropical crops. The regulatory role of SA in defending against chilling stress has been reported in many plant species, such as maize [25], mountain rye [26], watermelon [27], beans [28], wheat [29][30], and barley [31]. Furthermore, low temperatures induced the accumulation of endogenous SA in *Arabidopsis thaliana* and wheat plants, which further confirmed the relationship between SA and cold stress responses [30][32].

Low temperatures are effective for the storage of fruits and vegetables, but they may also cause chilling injury. SA as a highly efficient buffering agent against cold stress has been widely demonstrated in many fruits. For example, spraying 0.5 mM SA changed H₂O₂ metabolisms and increased the chilling tolerance of banana seedlings [33][34]. Similar results have been reported in cut flowers [35], bamboo shoots [36], as well as fruits in lemons [37][38], cucumbers [39], bell peppers [40], peaches [41][42], pomegranates [43][44], and plums [45].

1.3. Salinity

When grown in saline soils, plants may suffer from superabundant ion and osmotic stress, leading to ion imbalance and toxicity in plant cells [46]. It has been found that salt stress can cause a decrease in SA content in plants, such as *Iris hexagona* [47], tomato [48], and soybean [49], whereas the application of SA increased tolerance to salt toxicity in many plant species, such as pepper [50], cucumber [51], and soybean [52].

SA is an important regulator of influx and efflux of Na⁺. For instance, addition of SA to soil alleviated salt toxicity in maize by decreasing Na⁺ accumulation [53]. Exogenous foliar application of 1.5 mM SA reduced osmotic stress and improved the aerial K⁺/Na⁺ ratio of saffron under saline conditions [54]. Soaking seeds of *Leymus chinensis* in SA solution lowered osmotic damage on the plasma membrane by accumulating K⁺ and Ca²⁺ [55]. SA-signalled K⁺ accumulation might be due to the activation of H⁺-ATPase in the membrane [56], which occurs via guard cells outwardly rectifying K⁺ channel (GORK), as noted in *Arabidopsis thaliana* under salt stress [57]. The increase in Ca²⁺ influx in the cytoplasm may activate the transport system of Na⁺/H⁺ in the plasma membrane, which is mediated by the salt overly sensitive (SOS) signalling pathway [58]. Furthermore, the application of SA has been shown to maintain the membrane integrity by regulating compatible metabolites such as proline and soluble sugars. Irrigation of the solution with 1 mM SA into soil increased proline content and sustained membrane integrity of pepper cells [50]. Exogenous SA increases proline, soluble carbohydrates, and proteins contents in soybean leaves, thereby adjusting the water content of cells [56]. Pre-treatment of SA might induce a pre-adaptive response through a transient increase in H₂O₂ level, which may act as a second messenger to “set up” the plant to defend the following salt stress that may occur. Pre-treatment with SA enhances the activities of antioxidant enzymes in plants, which in turn decreases stress-induced oxidative stress, as has been noted in *Leymus chinensis* [55] and *Iris pseudacorus* [59]. The signalling role of SA is also cross-linked with ABA, glycinebetaine, and ethylene (ET), as they are closely correlated with the synthesis of stress proteins and maintenance of leaf water potential [60][61].

1.4. Metal Toxicity

Metal phytotoxicity has been a major subject of current plant biology research. Heavy metals can be absorbed easily by plant roots, transported into shoots, and cause various visible toxic symptoms, such as growth retardation, leaf chlorosis, wilting, and cell death. The beneficial role of SA in defence against metal toxicity has been reported in a wide range of plant species [62][63]. For instance, application of SA improved the growth and photosynthetic abilities in Pb-stressed rice [64], Cu-stressed *Phaseolus vulgaris* [65], and Ni-stressed mustard [66]. Recently, the co-reaction of SA with other promoters has also been evaluated. For example, combination exposure of SA and plant-growth-promoting bacteria reduced the Cr-induced oxidative damage in maize [67]. SA in combination with kinetin or calcium ameliorated Ni and Pb stress in *Phaseolus vulgaris* plants [68]. The combined supplementation of melatonin and SA effectively detoxified As toxicity by modulating phytochelatin and nitrogen metabolism in pepper plants [69].

Cadmium is one of the most toxic and widespread heavy metals in the world [70]. It is the typical toxic metal that can induce representative symptoms in plants, such as replacing and inactivating essential elements, destroying protein structure, and interfering with photosynthesis, respiration, and cell division [71]. A wide range of plant species have shown that SA is deeply involved in promoting Cd tolerance during processes such as plant growth, element assimilation, Cd translocation, photosynthesis, and senescence [71]. Therefore, this entry on the topic of metal toxicity is focused on the interaction of SA and Cd in plants.

The phytotoxicity of cadmium (Cd) is a major subject of current plant biology research. Recent studies have shown that the synthesis of SA in plants is markedly promoted by Cd stress. For example, after 25 μ M Cd treatment, the bound SA of maize was 10 times higher than that of untreated plants [72]. Similar phenomena have been observed in barley [73] and *Pisum sativum* [74]. Studies on a wide range of plant species have shown that SA is deeply involved in promoting Cd tolerance, including in plant growth, element assimilation, Cd translocation, photosynthesis, and senescence [71].

1.5. Other Stresses

1.5.1. Drought

During drought stress, plants have elevated SA levels, as noted in many plant species, such as barley [75], *Phillyrea angustifolia* [76], and *Salvia officinalis* [77]. The alleviation of drought injury by SA goes along with the hardening of the antioxidant system, increasing relative water and proline contents and regulating other phytohormones [78][79]. For example, pre-treatment of SA cleared the drought-induced superoxide radical with enhancement of the expression of redox regulating genes and increased proline content with its synthesis-related genes [80].

SA treatments effectively ameliorated the negative effects of drought through not only improving the photosynthetic performance and membrane permeability but also enhancing the activity of antioxidant enzymes. For instance, foliar application of SA substantially decreased the ROS and MDA contents of maize under drought stress [81]. Application of SA at 100 mM enhanced antioxidant enzymatic activities together with other physio-biochemical traits, such as membrane stability, chlorophyll content, and photosynthetic rates in wheat under drought stress [82]. When sprayed with SA at 0.5 mM, wheat seedlings effectively increased the activities of antioxidant enzymes (SOD, CAT, and PPO) to alleviate the drought-stress-induced damage effects [83]. Foliar spray of SA in sweet basil significantly promoted the plant growth and relative water contents under water-deficit conditions [84]. Spraying 2 mM SA into the leaves of *Rosmarinus officinalis* L. increased the production of essential oil under the mild drought stress (60% field capacity) [85]. Treatment with SA protected tomato plants from drought stress, mainly by maintaining membrane stability and activities of carbonic anhydrase that directly affect the rate of photosynthetic CO₂ fixation [86][87]. Pre-treatment with SA reduced damage to the cell membranes and increased ABA content in the leaves of barley and maize, suggesting that there is cross-talk between SA and ABA during drought stress [75][88].

1.5.2. Ozone

Ozone is a powerful oxidising agent that reacts with lipids and proteins in plant cells and causes oxidative damage [89][90]. SA deficiency in *NahG* plants is sensitive to the ozone, whereas ozone exposure stimulates SA accumulation and promotes virus resistance in tobacco [91]. Further evidence has shown that enhanced accumulation of SA by ozone stress is through the ICS pathway [92]. SA controls ET production of *Salvia officinalis* during ozone exposure by balancing cell redox and shrinking chlorosis formation in leaves [93]. However, abnormal levels of SA cause greater ozone injury either in deficiency or superfluosness. Many deficient genotypes, such as *Cvi-0*, *NahG*, *npr1*, *eds5*, and *sid2*, are sensitive to the ozone stress [94]. Exogenous SA application decreased the stomatal conductance, chlorophyll content, and Mg assimilation of rice under ozone stress [95]. Recently, an interesting study was conducted to test whether the O₃-induced cell death is regulated through SA, JA, or ethylene. The global and targeted analysis of transcriptional changes in single, double, and triple mutants mainly showed that the basal SA levels are essential for plants to defend against ROS-induced cell death, which is in conjunction with ethylene and JA signalling [96][97].

1.5.3. Pesticide

Some chemical pesticides, such as herbicide, also directly induced the oxidative damage in plants, as observed in cucumber, pistachio plants (*Pistacia vera* L.), and barley [98][99][100][101]. The injury caused by paraquat (a kind of herbicide) continuously generates superoxide in the chloroplasts of plant cells, motivates redox reaction chains, generates various forms of ROS, and leads to oxidative damage [99]. Transgenic *NahG* in rice plants causes SA deficiency, with lower glutathione (GSH) content showing great sensitivity to paraquat exposure [99]. SA significantly increases enzymatic parameters and photosynthetic pigments of *Vigna radiata* when exposed to fungicide (mancozeb), insecticide (chlorpyrifos), and herbicide (metribuzin) [102]. Pre-treatment with 1 mM SA triggers the activity and expression of pesticide detoxification enzymes (GSTs: glutathione S-transferases; a carbon-monoxide-bound enzyme, P450 (absorption band at 450 nm)) in thiram-treated leaves [103]. Treatment with 1 mM SA promotes the degradation of pesticides and blocks their accumulation in cucumber [104].

1.5.4. Ultraviolet Radiation

UV radiation a key environmental signal that influences plant growth and development and can reduce disease and pest incidence [105]. However, because it is beyond the capacity of sunlight utilisation in plants, excessive exposure can directly induce the ROS production, adversely affects photosynthesis, and damage cell membranes and proteins [102]. It has been shown that SA counteracted the UV-A-, UV-B-, and UV-C-induced oxidative stress on pepper through activating antioxidant enzymes such as POD, APX, CAT, and GR [106]. Furthermore, UV radiation activated SA defences and then enhanced the tomato resistance to pathogen attack in the JA-deficient genotype [107]. Similar to ozone, UV radiation induces SA accumulation in tobacco, which is accompanied by higher activity of benzoic acid 2-hydroxylase, a key enzyme in the catalysis of SA biosynthesis [91]. It has been found that exogenous SA alleviates the damaging effects of UV irradiance in many plant species such as blue grass, soybean, and maize [108][109]. The possible roles may include increase in anthocyanin and α -tocopherol content, photochemical efficiency, and activities of antioxidant enzymes.

2. Possible Mechanisms of SA in Mitigating Abiotic Stresses

Intensive research has shown that all abiotic stressors increase the level of endogenous SA, indicating that this simple molecule is involved in stress signalling in plants [110][111][112]. The regulatory roles of SA are mediated by various physiological processes, including growth development, photosynthesis, ion assimilation, respiration, antioxidant system, and cross-talk with other hormones [113]. The first report on the SA signalling is that it affects ROS production and then provokes pathogenesis-related1 (PR1) expression under pathogenic attack [114]. This discovery sparked the further studies on the complex signalling network between SA and ROS in plants [115]. Thus, the primary mechanism of SA reviewed here is its defensive role through redox signalling.

2.1. Redox Signalling

ROS are defined as the inevitable by-products of electron transfer in mitochondria, chloroplasts, and other energy-generating sites of plant cells [116]. Owing to their strong oxidisability, they can interfere with most biochemical metabolic processes, such as enzyme activity, membrane permeability, DNA stability, and protein synthesis. Under normal conditions, ROS are detoxified and maintained at equilibrium by the antioxidant defence system [117]. This system has experienced very complex evolutionary processes for 2.7 billion years. It is estimated that at least 152 genes in plants are involved in this highly dynamic and redundant network, which develops enzymatic and non-enzymatic compounds and encodes ROS-producing and -scavenging proteins [118] (See **Figure 1**). In many cases, the capacity to cease production of ROS is an important indicator of plant tolerance. Furthermore, low concentrations of ROS are successfully utilised by plants as a leading signalling pathway in physiological metabolic processes, such as growth development, hormone signalling, programmed cell death, cell cycle, and biotic and abiotic stress responses under normal and stress conditions [119].

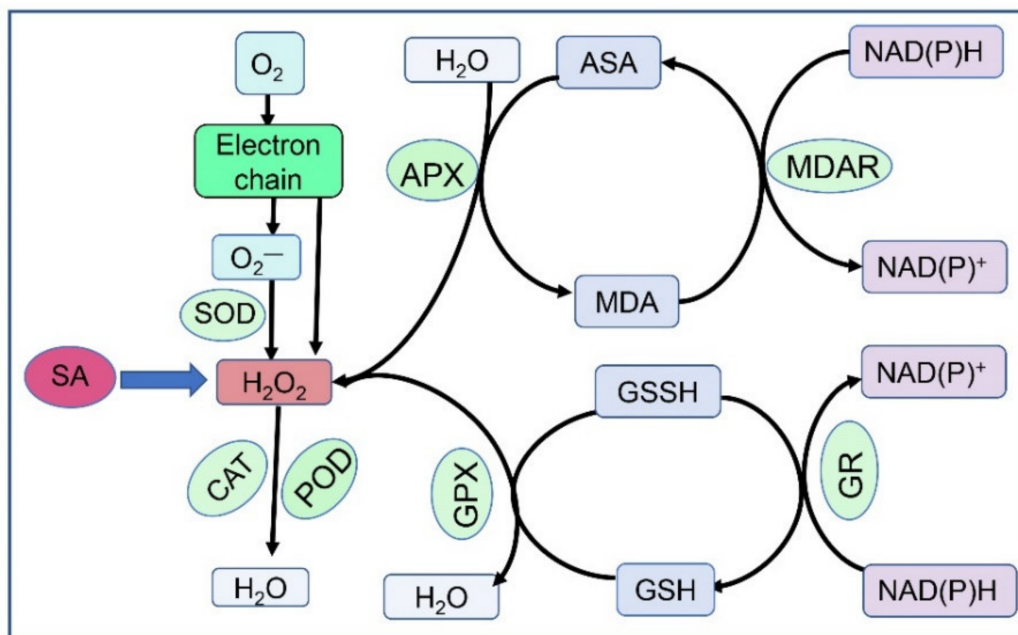


Figure 1. Brief pathways for reactive oxygen species scavenging in plants.

Although the benefits of SA signalling have been thoroughly studied, few studies have reported ambiguous results. SA treatment mitigated Cd toxicity in barley but failed to affect the activity of antioxidant enzymes [56]. High levels of SA promote the generation of H_2O_2 in leaves [120]. The results of studies on SA mutants are still contradictory. High SA levels

in *snc1* mutants generated a large amount of ROS, whereas SA deficiency in *NahG* lowered Cd-induced oxidative stress [121]. However, this finding is in contrast to the case of *sid2* mutants, in which Cd-induced oxidative damage was aggravated by the SA deficiency [122].

2.2. Cross-Talk with Other Plant Hormones

Besides of ROS, other plant hormones are involved in the SA signal transduction pathway of plants [123]. Most studies have observed a relationship between ABA and SA levels under stress. Treatment with SA induces ABA concentrations in barley and tomato [124]. Exposure of *Arabidopsis thaliana* leaves to ABA inhibits SA transduction both upstream and downstream through the SAR signalling pathway, and this suppressive effect is not related to jasmonate (JA)/ET-mediated signalling [125]. Similarly, salt stress increases the content of JA and ABA but decreases the levels of IAA, gibberellic acid (GA), and SA in *Iris hexagona* and soybean [47][49]. Insect feeding caused a strong accumulation of JA-specific mRNA transcripts, such as GmbPI1, GmKTI1, and GmAAT, but did not influence the free SA or SA-marker gene transcripts accumulation [126]. Drought stress increases the levels of SA and ABA in *Brassica napus*, and the effect on ABA is more pronounced [127]. However, the signalling role of SA might be stronger than that of ABA because the inhibition of SA biosynthesis leads to serious heating damage compared to the inhibition of ABA biosynthesis [128]. It seems that the biosynthesis of ABA is a downstream signalling event associated with SA sensing. Treatment with SA in salt-stressed tomato resulted in ABA accumulation in both root and leaf tissues together with upregulation of some ABA biosynthesis genes, such as SIZEP1, SINCED1, SIAO1, and SIAO2 [129]. In pea plants, the activity of SA glucosyl transferase may be inhibited by ABA, thus enhancing the concentrations of free SA [130].

Calcium (Ca^{2+}) is a key messenger in plants that can induce various defence responses against stress. SA-induced stomatal closure is associated with ABA signalling, and this process is mediated by Ca^{2+} / Ca^{2+} -dependent protein kinases (CPK) in *cpk3-2* and *cpk6-1* mutants but not in the Ca^{2+} -independent protein kinase Open Stomata1 (OST1) *ost1-3* mutant [131]. It was also observed that SA triggered the Ca^{2+} -sensing receptor in chloroplast thylakoid membranes of *Arabidopsis thaliana* [75]. Calmodulin, a Ca^{2+} -binding messenger protein, transduces Ca^{2+} signals by binding Ca^{2+} and then modifying the target proteins. The biosynthesis of SA is regulated by calmodulin-binding-protein (CBP60g) via the activation of isochorismate synthase 1 (ICS1) [132]. Recent studies in *Arabidopsis thaliana* have shown that the SA-signalled plant immunity is associated with calmodulin-binding transcription activators (CAMTA) [133].

Similar to the function of SA, nitric oxide plays a crucial role in controlling redox homeostasis in plant responses to abiotic stresses [134]. The application of SA and SNP (NO donor) significantly improved the heat-stress tolerance of hyacinth bean and Ni tolerance of finger millet [135]. Under As toxicity, the increase in NO concentration in rice is induced by SA through the enhancement of nitrate reductase activity [136]. SA increased As tolerance in maize by activating the antioxidant defence system, but this effect was completely negated when NO synthesis was blocked [137]. Furthermore, NO may act as a downstream signalling molecule that participates in SA-signalled cell wall construction, which could impede Cd influx in Cd-stressed rice seedlings [138]. Both NO and SA are involved in the signal transduction of stomatal closure, and the increase in NO levels is dependent on SA-induced NO synthase-like enzymes [139].

2.3. Mitogen-Activated Protein Kinase

Mitogen-activated protein kinase (MAPK) is a type of protein kinase that is specific to the threonine and amino acids serine, which is involved in cell functions and cellular responses to a diverse array of stimuli [140]. MPK3, MPK4, and MPK6 kinases are the main mediators of plant responses to biotic and abiotic stresses. Studies on *Arabidopsis thaliana* have shown that SA is involved in transmitting MAPKs cascade signalling [141]. Compared with the wild-type, approximately 50% of the basal expression level of AtMPK3 was noted in the SA-deficient mutants with low activity of AtMPK3 [142]. A 48-kD MAPKs in tobacco was identified by SA activation since it preferentially phosphorylates myelin basic protein (MBP) [143]. Conversely, MAPK regulated the levels of SA in stressed plants [144]. It was reported that SA treatment increased the TaMAPK4 transcripts in wheat under an avirulent race of pathogen attack, whereas knockdown the TaMAPK4 gene downregulated the SA accumulation [145]. Meanwhile, StMKK1 protein negatively regulated SA-related signalling pathways in defence against pathogens in potato [146]. *Mpk4* mutant accumulated excessive levels of SA, but this was not the reason for its extreme dwarf phenotype, as knocking down the ICS1 gene (SA synthesis) did not revert mpk4-impaired growth [147]. Furthermore, the accumulation of MPK4 might also be related to SA-regulated redox homeostasis, but this mechanism is still unknown and further study [148].

References

1. Bita, C.; Gerats, T. Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. *Front. Plant Sci.* 2013, 4, 273.
2. Yang, J.; Duan, L.; He, H.; Li, Y.; Li, X.; Liu, D.; Wang, J.; Jin, G.; Huang, S. Application of Exogenous KH_2PO_4 and Salicylic Acid and Optimization of the Sowing Date Enhance Rice Yield Under High-Temperature Conditions. *J. Plant Growth Regul.* 2022, 41, 1–15.
3. Pan, Q.; Zhan, J.; Liu, H.; Zhang, J.; Chen, J.; Wen, P.; Huang, W. Salicylic acid synthesized by benzoic acid 2-hydroxylase participates in the development of thermotolerance in pea plants. *Plant Sci.* 2006, 171, 226–233.
4. Dat, J.F.; Foyer, C.H.; Scott, I.M. Changes in salicylic acid and antioxidants during induced thermotolerance in mustard seedlings. *Plant Physiol.* 1998, 118, 1455–1461.
5. Larkindale, J.; Hall, J.D.; Knight, M.R.; Vierling, E. Heat stress phenotypes of Arabidopsis mutants implicate multiple signaling pathways in the acquisition of thermotolerance. *Plant Physiol.* 2005, 138, 882–897.
6. Wang, L.-J.; Li, S.-H. Thermotolerance and related antioxidant enzyme activities induced by heat acclimation and salicylic acid in grape (*Vitis vinifera* L.) leaves. *Plant Growth Regul.* 2006, 48, 137–144.
7. Widiastuti, A.; Yoshino, M.; Hasegawa, M.; Nitta, Y.; Sato, T. Heat shock-induced resistance increases chitinase-1 gene expression and stimulates salicylic acid production in melon (*Cucumis melo* L.). *Physiol. Mol. Plant Pathol.* 2013, 82, 51–55.
8. Čajánek, M.; Štroch, M.; Lachetova, I.; Kalina, J.; Spunda, V. Characterization of the photosystem II inactivation of heat-stressed barley leaves as monitored by the various parameters of chlorophyll a fluorescence and delayed fluorescence. *J. Photochem. Photobiol. B Biol.* 1998, 47, 39–45.
9. Wassie, M.; Zhang, W.; Zhang, Q.; Ji, K.; Cao, L.; Chen, L. Exogenous salicylic acid ameliorates heat stress-induced damages and improves growth and photosynthetic efficiency in alfalfa (*Medicago sativa* L.). *Ecotoxicol. Environ. Saf.* 2020, 191, 110206.
10. Shi, Q.; Bao, Z.; Zhu, Z.; Ying, Q.; Qian, Q. Effects of different treatments of salicylic acid on heat tolerance, chlorophyll fluorescence, and antioxidant enzyme activity in seedlings of *Cucumis sativa* L. *Plant Growth Regul.* 2006, 48, 127–135.
11. Wang, L.-J.; Fan, L.; Loescher, W.; Duan, W.; Liu, G.-J.; Cheng, J.-S.; Luo, H.-B.; Li, S.-H. Salicylic acid alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine leaves. *BMC Plant Biol.* 2010, 10, 34.
12. Afzal, I.; Akram, M.; Rehman, H.; Rashid, S.; Basra, S. Moringa leaf and sorghum water extracts and salicylic acid to alleviate impacts of heat stress in wheat. *S. Afr. J. Bot.* 2020, 129, 169–174.
13. Jahan, M.S.; Wang, Y.; Shu, S.; Zhong, M.; Chen, Z.; Wu, J.; Sun, J.; Guo, S. Exogenous salicylic acid increases the heat tolerance in Tomato (*Solanum lycopersicum* L.) by enhancing photosynthesis efficiency and improving antioxidant defense system through scavenging of reactive oxygen species. *Sci. Hortic.* 2019, 247, 421–429.
14. Khan, M.I.R.; Iqbal, N.; Masood, A.; Per, T.S.; Khan, N.A. Salicylic acid alleviates adverse effects of heat stress on photosynthesis through changes in proline production and ethylene formation. *Plant Signal. Behav.* 2013, 8, e26374.
15. Liu, Y.; Zhang, J.; Liu, H.; Huang, W. Salicylic acid or heat acclimation pre-treatment enhances the plasma membrane-associated ATPase activities in young grape plants under heat shock. *Sci. Hortic.* 2008, 119, 21–27.
16. Larkindale, J.; Knight, M.R. Protection against heat stress-induced oxidative damage in Arabidopsis involves calcium, abscisic acid, ethylene, and salicylic acid. *Plant Physiol.* 2002, 128, 682–695.
17. Clarke, S.M.; Mur, L.A.; Wood, J.E.; Scott, I.M. Salicylic acid dependent signaling promotes basal thermotolerance but is not essential for acquired thermotolerance in Arabidopsis thaliana. *Plant J.* 2004, 38, 432–447.
18. Cronjé, M.J.; Bornman, L. Salicylic acid influences Hsp70/Hsc70 expression in *Lycopersicon esculentum*: Dose- and time-dependent induction or potentiation. *Biochem. Biophys. Res. Commun.* 1999, 265, 422–427.
19. Snyman, M.; Cronjé, M. Modulation of heat shock factors accompanies salicylic acid-mediated potentiation of Hsp70 in tomato seedlings. *J. Exp. Bot.* 2008, 59, 2125–2132.
20. Chang, P.-F.L.; Jinn, T.-L.; Huang, W.-K.; Chen, Y.; Chang, H.-M.; Wang, C.-W. Induction of a cDNA clone from rice encoding a class II small heat shock protein by heat stress, mechanical injury, and salicylic acid. *Plant Sci.* 2007, 172, 64–75.
21. Liu, H.-T.; Huang, W.-D.; Pan, Q.-H.; Weng, F.-H.; Zhan, J.-C.; Liu, Y.; Wan, S.-B.; Liu, Y.-Y. Contributions of PIP2-specific-phospholipase C and free salicylic acid to heat acclimation-induced thermotolerance in pea leaves. *J. Plant Physiol.* 2006, 163, 405–416.

22. Li, Z.-G.; Xie, L.-R.; Li, X.-J. Hydrogen sulfide acts as a downstream signal molecule in salicylic acid-induced heat tolerance in maize (*Zea mays* L.) seedlings. *J. Plant Physiol.* 2015, 177, 121–127.
23. Dinler, B.; Demir, E.; Kompe, Y. Regulation of auxin, abscisic acid and salicylic acid levels by ascorbate application under heat stress in sensitive and tolerant maize leaves. *Acta Biol. Hung.* 2014, 65, 469–480.
24. Wang, L.-J.; Li, S.-H. Salicylic acid-induced heat or cold tolerance in relation to Ca^{2+} homeostasis and antioxidant systems in young grape plants. *Plant Sci.* 2006, 170, 685–694.
25. Janda, T.; Szalai, G.; Tari, I.; Paldi, E. Hydroponic treatment with salicylic acid decreases the effects of chilling injury in maize (*Zea mays* L.) plants. *Planta* 1999, 208, 175–180.
26. Ansari, O.; Sharif-Zadeh, F. Does Gibberellic acid (GA), Salicylic acid (SA) and Ascorbic acid (AsC) improve Mountain Rye (*Secale montanum*) seeds germination and seedlings growth under cold stress. *Int. Res. J. Appl. Basic Sci.* 2012, 3, 1651–1657.
27. Cheng, F.; Lu, J.; Gao, M.; Shi, K.; Kong, Q.; Huang, Y.; Bie, Z. Redox signaling and CBF-responsive pathway are involved in salicylic acid-improved photosynthesis and growth under chilling stress in watermelon. *Front. Plant Sci.* 2016, 7, 1519.
28. Gharib, F.; Hegazi, A. Salicylic acid ameliorates germination, seedling growth, phytohormone and enzymes activity in bean (*Phaseolus vulgaris* L.) under cold stress. *J. Am. Sci.* 2010, 6, 675–683.
29. Ignatenko, A.; Talanova, V.; Repkina, N.; Titov, A. Exogenous salicylic acid treatment induces cold tolerance in wheat through promotion of antioxidant enzyme activity and proline accumulation. *Acta Physiol. Plant.* 2019, 41, 1–10.
30. Kosová, K.; Prášil, I.T.; Vítámvás, P.; Dobrev, P.; Motyka, V.; Floková, K.; Novák, O.; Turečková, V.; Rolčík, J.; Pešek, B. Complex phytohormone responses during the cold acclimation of two wheat cultivars differing in cold tolerance, winter Samanta and spring Sandra. *J. Plant Physiol.* 2012, 169, 567–576.
31. Mutlu, S.; Karadağoglu, Ö.; Atici, Ö.; Nalbantoğlu, B. Protective role of salicylic acid applied before cold stress on antioxidant system and protein patterns in barley apoplast. *Biol. Plant.* 2013, 57, 507–513.
32. Scott, I.M.; Clarke, S.M.; Wood, J.E.; Mur, L.A. Salicylate accumulation inhibits growth at chilling temperature in *Arabidopsis*. *Plant Physiol.* 2004, 135, 1040–1049.
33. Kang, G.; Wang, C.; Sun, G.; Wang, Z. Salicylic acid changes activities of H_2O_2 -metabolizing enzymes and increases the chilling tolerance of banana seedlings. *Environ. Exp. Bot.* 2003, 50, 9–15.
34. Khademi, O.; Ashtari, M.; Razavi, F. Effects of salicylic acid and ultrasound treatments on chilling injury control and quality preservation in banana fruit during cold storage. *Sci. Hortic.* 2019, 249, 334–339.
35. Aghdam, M.S.; Jannatizadeh, A.; Sheikh-Assadi, M.; Malekzadeh, P. Alleviation of postharvest chilling injury in anthurium cut flowers by salicylic acid treatment. *Sci. Hortic.* 2016, 202, 70–76.
36. Luo, Z.; Wu, X.; Xie, Y.; Chen, C. Alleviation of chilling injury and browning of postharvest bamboo shoot by salicylic acid treatment. *Food Chem.* 2012, 131, 456–461.
37. Siboz, X.I.; Bertling, I.; Odindo, A.O. Salicylic acid and methyl jasmonate improve chilling tolerance in cold-stored lemon fruit (*Citrus limon*). *J. Plant Physiol.* 2014, 171, 1722–1731.
38. Siboz, X.I.; Bertling, I.; Odindo, A.O. Enzymatic antioxidants in response to methyl jasmonate and salicylic acid and their effect on chilling tolerance in lemon fruit. *Sci. Hortic.* 2017, 225, 659–667.
39. Zhang, Y.; Zhang, M.; Yang, H. Postharvest chitosan-g-salicylic acid application alleviates chilling injury and preserves cucumber fruit quality during cold storage. *Food Chem.* 2015, 174, 558–563.
40. Ge, W.; Zhao, Y.; Kong, X.; Sun, H.; Luo, M.; Yao, M.; Wei, B.; Ji, S. Combining salicylic acid and trisodium phosphate alleviates chilling injury in bell pepper (*Capsicum annuum* L.) through enhancing fatty-acid desaturation efficiency and water retention. *Food Chem.* 2020, 327, 127057.
41. Wang, L.; Chen, S.; Kong, W.; Li, S.; Archbold, D.D. Salicylic acid pretreatment alleviates chilling injury and affects the antioxidant system and heat shock proteins of peaches during cold storage. *Postharvest Biol. Technol.* 2006, 41, 244–251.
42. Cao, S.; Hu, Z.; Zheng, Y.; Lu, B. Synergistic effect of heat treatment and salicylic acid on alleviating internal browning in cold-stored peach fruit. *Postharvest Biol. Technol.* 2010, 58, 93–97.
43. Sayyari, M.; Castillo, S.; Valero, D.; Díaz-Mula, H.M.; Serrano, M. Acetyl salicylic acid alleviates chilling injury and maintains nutritive and bioactive compounds and antioxidant activity during postharvest storage of pomegranates. *Postharvest Biol. Technol.* 2011, 60, 136–142.
44. Sayyari, M.; Babalar, M.; Kalantari, S.; Serrano, M.; Valero, D. Effect of salicylic acid treatment on reducing chilling injury in stored pomegranates. *Postharvest Biol. Technol.* 2009, 53, 152–154.

45. Luo, Z.; Chen, C.; Xie, J. Effect of salicylic acid treatment on alleviating postharvest chilling injury of 'Qingnai' plum fruit. *Postharvest Biol. Technol.* 2011, 62, 115–120.
46. Zhao, C.; Zhang, H.; Song, C.; Zhu, J.-K.; Shabala, S. Mechanisms of plant responses and adaptation to soil salinity. *Innovation* 2020, 1, 100017.
47. Wang, Y.; Mopper, S.; Hasenstein, K.H. Effects of salinity on endogenous ABA, IAA, JA, and SA in *Iris hexagona*. *J. Chem. Ecol.* 2001, 27, 327–342.
48. Molina, A.; Bueno, P.; Marín, M.C.; Rodríguez-Rosales, M.P.; Belver, A.; Venema, K.; Donaire, J.P. Involvement of endogenous salicylic acid content, lipoxygenase and antioxidant enzyme activities in the response of tomato cell suspension cultures to NaCl. *N. Phytol.* 2002, 156, 409–415.
49. Hamayun, M.; Khan, S.A.; Khan, A.L.; Shinwari, Z.K.; Hussain, J.; Sohn, E.-Y.; Kang, S.-M.; Kim, Y.-H.; Khan, M.A.; Lee, I.-J. Effect of salt stress on growth attributes and endogenous growth hormones of soybean cultivar Hwangkeumkong. *Pak. J. Bot.* 2010, 42, 3103–3112. Available online: [https://www.pakbs.org/pjbot/PDFs/42\(5\)/PJB42\(5\)3103.pdf](https://www.pakbs.org/pjbot/PDFs/42(5)/PJB42(5)3103.pdf) (accessed on 10 June 2022).
50. Kumar, S.; Abass Ahanger, M.; Alshaya, H.; Latief Jan, B.; Yerramilli, V. Salicylic acid mitigates salt induced toxicity through the modifications of biochemical attributes and some key antioxidants in *capsicum annuum*. *Saudi J. Biol. Sci.* 2022, 29, 1337–1347.
51. Chojak-Koźniewska, J.; Linkiewicz, A.; Sowa, S.; Radzioch, M.; Kuźniak, E. Interactive effects of salt stress and *Pseudomonas syringae* pv. *lachrymans* infection in cucumber: Involvement of antioxidant enzymes, abscisic acid and salicylic acid. *Environ. Exp. Bot.* 2017, 136, 9–20.
52. Farhangi-Abriz, S.; Ghassemi-Golezani, K. How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants? *Ecotoxicol. Environ. Saf.* 2018, 147, 1010–1016.
53. Gunes, A.; Inal, A.; Alpaslan, M.; Eraslan, F.; Bagci, E.G.; Cicek, N. Salicylic acid induced changes on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays* L.) grown under salinity. *J. Plant Physiol.* 2007, 164, 728–736.
54. Feizi, H.; Moradi, R.; Pourghasemian, N.; Sahabi, H. Assessing saffron response to salinity stress and alleviating potential of gamma amino butyric acid, salicylic acid and vermicompost extract on salt damage. *S. Afr. J. Bot.* 2021, 141, 330–343.
55. Hongna, C.; Leyuan, T.; Junmei, S.; Xiaori, H.; Xianguo, C. Exogenous salicylic acid signal reveals an osmotic regulatory role in priming the seed germination of *leymus chinensis* under salt-alkali stress. *Environ. Exp. Bot.* 2021, 188, 104498.
56. Ghassemi-Golezani, K.; Farhangi-Abriz, S. Foliar sprays of salicylic acid and jasmonic acid stimulate H⁺-ATPase activity of tonoplast, nutrient uptake and salt tolerance of soybean. *Ecotoxicol. Environ. Saf.* 2018, 166, 18–25.
57. Jayakannan, M.; Bose, J.; Babourina, O.; Rengel, Z.; Shabala, S. Salicylic acid improves salinity tolerance in *Arabidopsis* is by restoring membrane potential and preventing salt-induced K⁺ loss via a GORK channel. *J. Exp. Bot.* 2013, 64, 2255–2268.
58. Sun, J.; Wang, M.J.; Ding, M.Q.; Deng, S.R.; Liu, M.Q.; Lu, C.F.; Zhou, X.Y.; Shen, X.; Zheng, X.J.; Zhang, Z.K. H₂O₂ and cytosolic Ca²⁺ signals triggered by the PM H⁺-coupled transport system mediate K⁺/Na⁺ homeostasis in NaCl-stressed *Populus euphratica* cells. *Plant Cell Environ.* 2010, 33, 943–958.
59. Liu, T.; Li, T.; Zhang, L.; Li, H.; Liu, S.; Yang, S.; An, Q.; Pan, C.; Zou, N. Exogenous salicylic acid alleviates the accumulation of pesticides and mitigates pesticide-induced oxidative stress in cucumber plants (*Cucumis sativus* L.). *Ecotoxicol. Environ. Saf.* 2021, 208, 111654.
60. Khan, M.I.R.; Asgher, M.; Khan, N.A. Alleviation of salt-induced photosynthesis and growth inhibition by salicylic acid involves glycinebetaine and ethylene in mungbean (*Vigna radiata* L.). *Plant Physiol. Biochem.* 2014, 80, 67–74.
61. Shakirova, F.M.; Sakhabutdinova, A.R.; Bezrukova, M.V.; Fatkhutdinova, R.A.; Fatkhutdinova, D.R. Changes in the hormonal status of wheat seedlings induced by salicylic acid and salinity. *Plant Sci.* 2003, 164, 317–322.
62. Yadav, V.; Arif, N.; Kováč, J.; Singh, V.P.; Tripathi, D.K.; Chauhan, D.K.; Vaculík, M. Structural modifications of plant organs and tissues by metals and metalloids in the environment: A review. *Plant Physiol. Biochem.* 2021, 159, 100–112.
63. Huihui, Z.; Xin, L.; Zisong, X.; Yue, W.; Zhiyuan, T.; Meijun, A.; Yuehui, Z.; Wenxu, Z.; Nan, X.; Guangyu, S. Toxic effects of heavy metals Pb and Cd on mulberry (*Morus alba* L.) seedling leaves: Photosynthetic function and reactive oxygen species (ROS) metabolism responses. *Ecotoxicol. Environ. Saf.* 2020, 195, 110469.
64. Jing, C.; Cheng, Z.; Li, L.-P.; Sun, Z.-Y.; Pan, X.-B. Effects of exogenous salicylic acid on growth and H₂O₂-metabolizing enzymes in rice seedlings under lead stress. *J. Environ. Sci.* 2007, 19, 44–49.

65. Zengin, F. Exogenous treatment with salicylic acid alleviating copper toxicity in bean seedlings. *Proc. Natl. Acad. Sci. India Sect. B Biol. Sci.* 2014, 84, 749–755.
66. Zaid, A.; Mohammad, F.; Wani, S.H.; Siddique, K.M. Salicylic acid enhances nickel stress tolerance by up-regulating antioxidant defense and glyoxalase systems in mustard plants. *Ecotoxicol. Environ. Saf.* 2019, 180, 575–587.
67. Islam, F.; Yasmeen, T.; Arif, M.S.; Riaz, M.; Shahzad, S.M.; Imran, Q.; Ali, I. Combined ability of chromium (Cr) tolerant plant growth promoting bacteria (PGPB) and salicylic acid (SA) in attenuation of chromium stress in maize plants. *Plant Physiol. Biochem.* 2016, 108, 456–467.
68. Khalil, R.; Haroun, S.; Bassyoini, F.; Nagah, A.; Yusuf, M. Salicylic acid in combination with kinetin or calcium ameliorates heavy metal stress in *Phaseolus vulgaris* plant. *J. Agric. Food Res.* 2021, 5, 100182.
69. Kaya, C.; Sarioglu, A.; Ashraf, M.; Alyemeni, M.N.; Ahmad, P. The combined supplementation of melatonin and salicylic acid effectively detoxifies arsenic toxicity by modulating phytochelators and nitrogen metabolism in pepper plants. *Environ. Pollut.* 2022, 297, 118727.
70. Huybrechts, M.; Cuypers, A.; Deckers, J.; Iven, V.; Vandionant, S.; Jozefczak, M.; Hendrix, S. Cadmium and plant development: An agony from seed to seed. *Int. J. Mol. Sci.* 2019, 20, 3971.
71. Guo, B.; Liu, C.; Liang, Y.; Li, N.; Fu, Q. Salicylic acid signals plant defence against cadmium toxicity. *Int. J. Mol. Sci.* 2019, 20, 2960.
72. Krantev, A.; Yordanova, R.; Janda, T.; Szalai, G.; Popova, L. Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. *J. Plant Physiol.* 2008, 165, 920–931.
73. Metwally, A.; Finkemeier, I.; Georgi, M.; Dietz, K.-J. Salicylic acid alleviates the cadmium toxicity in barley seedlings. *Plant Physiol.* 2003, 132, 272–281.
74. Metwally, A.; Safronova, V.I.; Belimov, A.A.; Dietz, K.-J. Genotypic variation of the response to cadmium toxicity in *Pisum sativum* L. *J. Exp. Bot.* 2005, 56, 167–178.
75. Bandurska, H. The effect of salicylic acid on barley response to water deficit. *Acta Physiol. Plant.* 2005, 27, 379–386.
76. Munne-Bosch, S.; Penuelas, J. Photo- and antioxidative protection, and a role for salicylic acid during drought and recovery in field-grown *Phillyrea angustifolia* plants. *Planta* 2003, 217, 758–766.
77. Abreu, M.E.; Munne-Bosch, S. Salicylic acid may be involved in the regulation of drought-induced leaf senescence in perennials: A case study in field-grown *Salvia officinalis* L. plants. *Environ. Exp. Bot.* 2008, 64, 105–112.
78. Arif, Y.; Sami, F.; Siddiqui, H.; Bajguz, A.; Hayat, S. Salicylic acid in relation to other phytohormones in plant: A study towards physiology and signal transduction under challenging environment. *Environ. Exp. Bot.* 2020, 175, 104040.
79. Safari, M.; Mousavi-Fard, S.; Rezaei Nejad, A.; Sorkheh, K.; Sofo, A. Exogenous salicylic acid positively affects morpho-physiological and molecular responses of *Impatiens walleriana* plants grown under drought stress. *Int. J. Environ. Sci. Technol.* 2021, 19, 969–984.
80. Lee, B.-R.; Islam, M.T.; Park, S.-H.; Jung, H.-i.; Bae, D.-W.; Kim, T.-H. Characterization of salicylic acid-mediated modulation of the drought stress responses: Reactive oxygen species, proline, and redox state in *Brassica napus*. *Environ. Exp. Bot.* 2019, 157, 1–10.
81. Shemi, R.; Wang, R.; Gheith, E.-S.; Hussain, H.A.; Hussain, S.; Irfan, M.; Cholidah, L.; Zhang, K.; Zhang, S.; Wang, L. Effects of salicylic acid, zinc and glycine betaine on morpho-physiological growth and yield of maize under drought stress. *Sci. Rep.* 2021, 11, 3195.
82. Ahmad, A.; Aslam, Z.; Naz, M.; Hussain, S.; Javed, T.; Aslam, S.; Raza, A.; Ali, H.M.; Siddiqui, M.H.; Salem, M.Z. Exogenous salicylic acid-induced drought stress tolerance in wheat (*Triticum aestivum* L.) grown under hydroponic culture. *PLoS ONE* 2021, 16, e0260556.
83. Khalvandi, M.; Siosemardeh, A.; Roohi, E.; Keramati, S. Salicylic acid alleviated the effect of drought stress on photosynthetic characteristics and leaf protein pattern in winter wheat. *Heliyon* 2021, 7, e05908.
84. Damalas, C.A. Improving drought tolerance in sweet basil (*Ocimum basilicum*) with salicylic acid. *Sci. Hortic.* 2019, 246, 360–365.
85. Abbaszadeh, B.; Layeghbaghi, M.; Azimi, R.; Hadi, N. Improving water use efficiency through drought stress and using salicylic acid for proper production of *Rosmarinus officinalis* L. *Ind. Crops Prod.* 2020, 144, 111893.
86. Tiwari, A.; Kumar, P.; Singh, S.; Ansari, S. Carbonic anhydrase in relation to higher plants. *Photosynthetica* 2005, 43, 1–11.
87. Hayat, S.; Hasan, S.A.; Fariduddin, Q.; Ahmad, A. Growth of tomato (*Lycopersicon esculentum*) in response to salicylic acid under water stress. *J. Plant Interact.* 2008, 3, 297–304.

88. Tayyab, N.; Naz, R.; Yasmin, H.; Nosheen, A.; Keyani, R.; Sajjad, M.; Hassan, M.N.; Roberts, T.H. Combined seed and foliar pre-treatments with exogenous methyl jasmonate and salicylic acid mitigate drought-induced stress in maize. *PLoS ONE* 2020, 15, e0232269.
89. Wedow, J.M.; Ainsworth, E.A.; Li, S. Plant biochemistry influences tropospheric ozone formation, destruction, deposition, and response. *Trends Biochem. Sci.* 2021, 46, 992–1002.
90. Oksanen, E.; Pandey, V.; Pandey, A.; Keski-Saari, S.; Kontunen-Soppela, S.; Sharma, C. Impacts of increasing ozone on Indian plants. *Environ. Pollut.* 2013, 177, 189–200.
91. Yalpani, N.; Enyedi, A.J.; León, J.; Raskin, I. Ultraviolet light and ozone stimulate accumulation of salicylic acid, pathogenesis-related proteins and virus resistance in tobacco. *Planta* 1994, 193, 372–376.
92. Ogawa, D.; Nakajima, N.; Tamaoki, M.; Aono, M.; Kubo, A.; Kamada, H.; Saji, H. The isochorismate pathway is negatively regulated by salicylic acid signaling in O₃-exposed *Arabidopsis*. *Planta* 2007, 226, 1277–1285.
93. Pellegrini, E.; Trivellini, A.; Cotozzzi, L.; Vernieri, P.; Nali, C. Involvement of Phytohormones in Plant Responses to Ozone. In *Plant Hormones under Challenging Environmental Factors*; Springer: Berlin, Germany, 2016; pp. 215–245.
94. Marchica, A.; Cotozzzi, L.; Lorenzini, G.; Nali, C.; Pellegrini, E. Antioxidants and Phytohormones Act in Coordination to Regulate Sage Response to Long Term Ozone Exposure. *Plants* 2022, 11, 904.
95. Rao, M.V.; Davis, K.R. Ozone-induced cell death occurs via two distinct mechanisms in *Arabidopsis*: The role of salicylic acid. *Plant J.* 1999, 17, 603–614.
96. Xu, E.; Vaahtera, L.; Brosché, M. Roles of defense hormones in the regulation of ozone-induced changes in gene expression and cell death. *Mol. Plant* 2015, 8, 1776–1794.
97. Kittipornkul, P.; Treesubsuntorn, C.; Thiravetyan, P. Effect of exogenous catechin and salicylic acid on rice productivity under ozone stress: The role of chlorophyll contents, lipid peroxidation, and antioxidant enzymes. *Environ. Sci. Pollut. Res.* 2020, 27, 25774–25784.
98. Dubey, P.; Mishra, A.K.; Singh, A.K. Comparative analyses of genotoxicity, oxidative stress and antioxidative defence system under exposure of methyl parathion and hexaconazole in barley (*Hordeum vulgare* L.). *Environ. Sci. Pollut. Res.* 2015, 22, 19848–19859.
99. Homayonzadeh, M.; Hosseiniaveh, V.; Haghighi, S.R.; Talebi, K.; Roessner, U.; Maali-Amiri, R. Evaluation of physiological and biochemical responses of pistachio plants (*Pistacia vera* L.) exposed to pesticides. *Ecotoxicology* 2021, 30, 1084–1097.
100. Huang, Y.; Adeleye, A.S.; Zhao, L.; Minakova, A.S.; Anumol, T.; Keller, A.A. Antioxidant response of cucumber (*Cucumis sativus*) exposed to nano copper pesticide: Quantitative determination via LC-MS/MS. *Food Chem.* 2019, 270, 47–52.
101. Homayonzadeh, M.; Moeini, P.; Talebi, K.; Roessner, U.; Hosseiniaveh, V. Antioxidant system status of cucumber plants under pesticides treatment. *Acta Physiol. Plant.* 2020, 42, 1–11.
102. Fatma, F.; Kamal, A.; Srivastava, A. Exogenous application of salicylic acid mitigates the toxic effect of pesticides in *Vigna radiata* (L.) Wilczek. *J. Plant Growth Regul.* 2018, 37, 1185–1194.
103. Nazish, T.; Huang, Y.-J.; Zhang, J.; Xia, J.-Q.; Alfatih, A.; Luo, C.; Cai, X.-T.; Xi, J.; Xu, P.; Xiang, C.-B. Understanding paraquat resistance mechanisms in *Arabidopsis thaliana* to facilitate developing paraquat-resistant crops. *Plant Commun.* 2022, 3, 100321.
104. Kusumi, K.; Yaeno, T.; Kojo, K.; Hirayama, M.; Hirokawa, D.; Yara, A.; Iba, K. The role of salicylic acid in the glutathione-mediated protection against photooxidative stress in rice. *Physiol. Plant.* 2006, 128, 651–661.
105. Meyer, P.; Van de Poel, B.; De Coninck, B. UV-B light and its application potential to reduce disease and pest incidence in crops. *Hortic. Res.* 2021, 8, 194.
106. Mahdavian, K.; Ghorbanli, M.; Kalantari, K.M. Role of salicylic acid in regulating ultraviolet radiation-induced oxidative stress in pepper leaves. *Russ. J. Plant Physiol.* 2008, 55, 560–563.
107. Escobar Bravo, R.; Chen, G.; Grosser, K.; Van Dam, N.M.; Leiss, K.A.; Klinkhamer, P.G. Ultraviolet radiation enhances salicylic acid-mediated defense signaling and resistance to *Pseudomonas syringae* DC3000 in a jasmonic acid-deficient tomato mutant. *Plant Signal. Behav.* 2019, 14, e1581560.
108. Yüzbaşıoğlu, E.; Dalyan, E. Salicylic acid alleviates thiram toxicity by modulating antioxidant enzyme capacity and pesticide detoxification systems in the tomato (*Solanum lycopersicum* Mill.). *Plant Physiol. Biochem.* 2019, 135, 322–330.
109. Liu, T.; Yuan, C.; Gao, Y.; Luo, J.; Yang, S.; Liu, S.; Zhang, R.; Zou, N. Exogenous salicylic acid mitigates the accumulation of some pesticides in cucumber seedlings under different cultivation methods. *Ecotoxicol. Environ. Saf.* 2020, 198, 110680.

110. Khan, M.I.R.; Fatma, M.; Per, T.S.; Anjum, N.A.; Khan, N.A. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. *Front. Plant Sci.* 2015, 6, 462.
111. Santisree, P.; Jalli, L.C.L.; Bhatnagar-Mathur, P.; Sharma, K.K. Emerging roles of salicylic acid and jasmonates in plant abiotic stress responses. In *Protective Chemical Agents in the Amelioration of Plant Abiotic Stress*; Wiley: Hoboken, NJ, USA, 2020; pp. 342–373.
112. Ahmad, F.; Singh, A.; Kamal, A. Salicylic Acid-Mediated Defense Mechanisms to Abiotic Stress Tolerance. In *Plant Signaling Molecules*; Woodhead Publishing: Sawston, UK, 2019; pp. 355–369.
113. Rivas-San Vicente, M.; Plasencia, J. Salicylic acid beyond defence: Its role in plant growth and development. *J. Exp. Bot.* 2011, 62, 3321–3338.
114. Rajendiran, K.; Ramanujam, M. Alleviation of ultraviolet-B radiation-induced growth inhibition of green gram by triadimefon. *Biol. Plant.* 2003, 46, 621–624.
115. Del Valle, J.C.; Buide, M.L.; Whittall, J.B.; Valladares, F.; Narbona, E. UV radiation increases phenolic compound protection but decreases reproduction in *Silene littorea*. *PLoS ONE* 2020, 15, e0231611.
116. Kosobryukhov, A.; Khudyakova, A.; Kreslavski, V. Impact of UV radiation on photosynthetic apparatus: Adaptive and damaging mechanisms. In *Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives I*; Springer: Berlin, Germany, 2020; pp. 555–576.
117. Kovacs, E.; Keresztes, A. Effect of gamma and UV-B/C radiation on plant cells. *Micron* 2002, 33, 199–210.
118. Hideg, É.; Jansen, M.A.; Strid, Å. UV-B exposure, ROS, and stress: Inseparable companions or loosely linked associates? *Trends Plant Sci.* 2013, 18, 107–115.
119. Singh, V.P.; Kumar, J.; Singh, M.; Singh, S.; Prasad, S.M.; Dwivedi, R.; Singh, M. Role of salicylic acid-seed priming in the regulation of chromium (VI) and UV-B toxicity in maize seedlings. *Plant Growth Regul.* 2016, 78, 79–91.
120. Rao, M.V.; Paliyath, G.; Ormrod, D.P.; Murr, D.P.; Watkins, C.B. Influence of salicylic acid on H₂O₂ production, oxidative stress, and H₂O₂-metabolizing enzymes (salicylic acid-mediated oxidative damage requires H₂O₂). *Plant Physiol.* 1997, 115, 137–149.
121. Li, X.; Clarke, J.D.; Zhang, Y.; Dong, X. Activation of an EDS1-mediated R-gene pathway in the *snc1* mutant leads to constitutive, NPR1-independent pathogen resistance. *Mol. Plant-Microbe Interact.* 2001, 14, 1131–1139.
122. Petersen, M.; Brodersen, P.; Naested, H.; Andreasson, E.; Lindhart, U.; Johansen, B.; Nielsen, H.B.; Lacy, M.; Austin, M.J.; Parker, J.E. Arabidopsis map kinase 4 negatively regulates systemic acquired resistance. *Cell* 2000, 103, 1111–1120.
123. Han, Y.; Chaouch, S.; Mhamdi, A.; Queval, G.; Zechmann, B.; Noctor, G. Functional analysis of Arabidopsis mutants points to novel roles for glutathione in coupling H₂O₂ to activation of salicylic acid accumulation and signaling. *Antioxid. Redox Signal.* 2013, 18, 2106–2121.
124. Freeman, J.L.; Garcia, D.; Kim, D.; Hopf, A.; Salt, D.E. Constitutively elevated salicylic acid signals glutathione-mediated nickel tolerance in *Thlaspi* nickel hyperaccumulators. *Plant Physiol.* 2005, 137, 1082–1091.
125. Guan, C.; Ji, J.; Jia, C.; Guan, W.; Li, X.; Jin, C.; Wang, G. A GSHS-like gene from *Lycium chinense* maybe regulated by cadmium-induced endogenous salicylic acid and overexpression of this gene enhances tolerance to cadmium stress in Arabidopsis. *Plant Cell Rep.* 2015, 34, 871–884.
126. Beyer, S.F.; Bel, P.S.; Flors, V.; Schultheiss, H.; Conrath, U.; Langenbach, C.J. Disclosure of salicylic acid and jasmonic acid-responsive genes provides a molecular tool for deciphering stress responses in soybean. *Sci. Rep.* 2021, 11, 20600.
127. Chaouch, S.; Queval, G.; Vanderauwera, S.; Mhamdi, A.; Vandorpe, M.; Langlois-Meurinne, M.; Van Breusegem, F.; Sandrean, P.; Noctor, G. Peroxisomal hydrogen peroxide is coupled to biotic defense responses by ISOCHORISMATE Synthase1 in a daylength-related manner. *Plant Physiol.* 2010, 153, 1692–1705.
128. Chang, C.C.; Slesak, I.; Jordá, L.; Sotnikov, A.; Melzer, M.; Miszalski, Z.; Mullineaux, P.M.; Parker, J.E.; Karpinska, B.; Karpinski, S. Arabidopsis chloroplastic glutathione peroxidases play a role in cross talk between photooxidative stress and immune responses. *Plant Physiol.* 2009, 150, 670–683.
129. Moons, A. Osgtu3 and osgtu4, encoding tau class glutathione S-transferases, are heavy metal- and hypoxic stress-induced and differentially salt stress-responsive in rice roots. *FEBS Lett.* 2003, 553, 427–432.
130. Garretón, V.; Carpinelli, J.; Jordana, X.; Holuigue, L. The as-1 promoter element is an oxidative stress-responsive element and salicylic acid activates it via oxidative species. *Plant Physiol.* 2002, 130, 1516–1526.
131. Sappl, P.G.; Oñate-Sánchez, L.; Singh, K.B.; Millar, A.H. Proteomic analysis of glutathione S-transferases of Arabidopsis thaliana reveals differential salicylic acid-induced expression of the plant-specific phi and tau classes. *Plant Mol. Biol.*

132. Yasuda, M.; Ishikawa, A.; Jikumaru, Y.; Seki, M.; Umezawa, T.; Asami, T.; Maruyama-Nakashita, A.; Kudo, T.; Shinozaki, K.; Yoshida, S. Antagonistic interaction between systemic acquired resistance and the abscisic acid-mediated abiotic stress response in *Arabidopsis*. *Plant Cell* 2008, 20, 1678–1692.
133. Park, S.-H.; Lee, B.-R.; Al Mamun, M.; Bae, D.-W.; Kim, T.-H. Characterization of salicylic acid-and abscisic acid-mediated photosynthesis, Ca^{2+} and H_2O_2 accumulation in two distinct phases of drought stress intensity in *Brassica napus*. *Environ. Exp. Bot.* 2021, 186, 104434.
134. Liu, H.-T.; Liu, Y.-Y.; Pan, Q.-H.; Yang, H.-R.; Zhan, J.-C.; Huang, W.-D. Novel interrelationship between salicylic acid, abscisic acid, and PIP2-specific phospholipase C in heat acclimation-induced thermotolerance in pea leaves. *J. Exp. Bot.* 2006, 57, 3337–3347.
135. Horváth, E.; Csiszár, J.; Gallé, Á.; Poór, P.; Szepesi, Á.; Tari, I. Hardening with salicylic acid induces concentration-dependent changes in abscisic acid biosynthesis of tomato under salt stress. *J. Plant Physiol.* 2015, 183, 54–63.
136. Prodhon, M.Y.; Munemasa, S.; Nahar, M.N.-E.-N.; Nakamura, Y.; Murata, Y. Guard cell salicylic acid signaling is integrated into abscisic acid signaling via the Ca^{2+} /CPK-dependent pathway. *Plant Physiol.* 2018, 178, 441–450.
137. Nomura, H.; Komori, T.; Uemura, S.; Kanda, Y.; Shimotani, K.; Nakai, K.; Furuichi, T.; Takebayashi, K.; Sugimoto, T.; Sano, S. Chloroplast-mediated activation of plant immune signalling in *Arabidopsis*. *Nat. Commun.* 2012, 3, 926.
138. Sun, T.; Huang, J.; Xu, Y.; Verma, V.; Jing, B.; Sun, Y.; Orduna, A.R.; Tian, H.; Huang, X.; Xia, S. Redundant CAMTA transcription factors negatively regulate the biosynthesis of salicylic acid and N-hydroxy-pipecolic acid by modulating the expression of SARD1 and CBP60g. *Mol. Plant* 2020, 13, 144–156.
139. Kim, Y.; Gilmour, S.J.; Chao, L.; Park, S.; Thomashow, M.F. *Arabidopsis* CAMTA transcription factors regulate pipecolic acid biosynthesis and priming of immunity genes. *Mol. Plant* 2020, 13, 157–168.
140. Wei, L.; Zhang, M.; Wei, S.; Zhang, J.; Wang, C.; Liao, W. Roles of nitric oxide in heavy metal stress in plants: Cross-talk with phytohormones and protein S-nitrosylation. *Environ. Pollut.* 2020, 259, 113943.
141. Rai, K.K.; Rai, N.; Rai, S.P. Salicylic acid and nitric oxide alleviate high temperature induced oxidative damage in *Lablab purpureus* L plants by regulating bio-physical processes and DNA methylation. *Plant Physiol. Biochem.* 2018, 128, 72–88.
142. Kotapati, K.V.; Palaka, B.K.; Ampasala, D.R. Alleviation of nickel toxicity in finger millet (*Eleusine coracana* L.) germinating seedlings by exogenous application of salicylic acid and nitric oxide. *Crop J.* 2017, 5, 240–250.
143. Singh, A.P.; Dixit, G.; Kumar, A.; Mishra, S.; Kumar, N.; Dixit, S.; Singh, P.K.; Dwivedi, S.; Trivedi, P.K.; Pandey, V. A protective role for nitric oxide and salicylic acid for arsenite phytotoxicity in rice (*Oryza sativa* L.). *Plant Physiol. Biochem.* 2017, 115, 163–173.
144. Kaya, C.; Ashraf, M.; Alyemeni, M.N.; Corpas, F.J.; Ahmad, P. Salicylic acid-induced nitric oxide enhances arsenic toxicity tolerance in maize plants by upregulating the ascorbate-glutathione cycle and glyoxalase system. *J. Hazard. Mater.* 2020, 399, 123020.
145. Wang, B.; Song, N.; Zhang, Q.; Wang, N.; Kang, Z. TaMAPK4 acts as a positive regulator in defense of wheat stripe rust infection. *Front. Plant Sci.* 2018, 9, 152.
146. Zhang, H.; Li, F.; Li, Z.; Cheng, J.; Chen, X.; Wang, Q.; Joosten, M.H.; Shan, W.; Du, Y. Potato StMPK7 is a downstream component of StMKK1 and promotes resistance to the oomycete pathogen *Phytophthora infestans*. *Mol. Plant Pathol.* 2021, 22, 644–657.
147. Pan, J.; Guan, M.; Xu, P.; Chen, M.; Cao, Z. Salicylic acid reduces cadmium (Cd) accumulation in rice (*Oryza sativa* L.) by regulating root cell wall composition via nitric oxide signaling. *Sci. Total Environ.* 2021, 797, 149202.
148. Agurla, S.; Sunitha, V.; Raghavendra, A.S. Methyl salicylate is the most effective natural salicylic acid ester to close stomata while raising reactive oxygen species and nitric oxide in *Arabidopsis* guard cells. *Plant Physiol. Biochem.* 2020, 157, 276–283.