

# NO Signaling/ROS during Abiotic Stresses

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With the rapidly growing human population and changing global climate conditions, it is critical to prevent global crop losses to meet the increasing demand for food and other crop products. The reactive gaseous signaling molecule nitric oxide (NO) is involved in numerous plant developmental processes as well as plant responses to various abiotic stresses through its interactions with various molecules. Together, these interactions lead to the homeostasis of reactive oxygen species (ROS), proline and glutathione biosynthesis, post-translational modifications such as S-nitrosylation, and modulation of gene and protein expression. Exogenous application of various NO donors positively mitigates the negative effects of various abiotic stressors.

Keywords: abiotic stress ; nitric oxide (NO) ; drought stress ; heavy metal stress ; soil salinity ; reactive oxygen species (ROS) ; plant stress

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## 1. Introduction

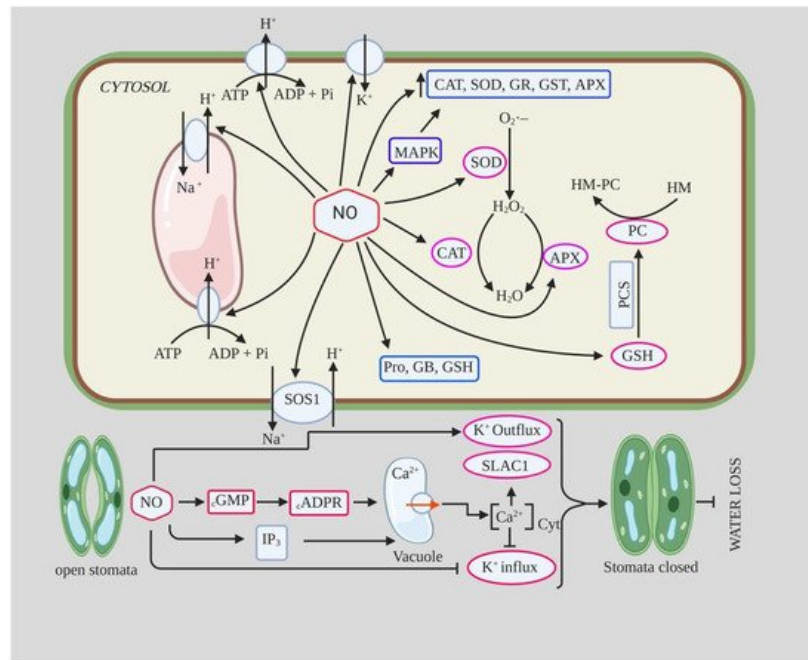
Various abiotic stressors such as heavy metals, high salinity, high or low temperature, UV radiation, and drought pose serious threats to plants and are detrimental to agriculture and the ecosystem, resulting in major losses <sup>[1][2]</sup>. Due to their sessile nature, plants have to counteract these stressors by developing effective strategies during evolution to survive in these harsh conditions. Under such conditions, plants initiate various responses at molecular, physiological, and cellular levels <sup>[3][4]</sup>. A common and convergent plant response to abiotic stresses is the production of redox molecules, including reactive oxygen species (ROS) and reactive nitrogen species (RNS) <sup>[5]</sup>.

ROS (e.g., singlet oxygen, hydrogen peroxide, superoxide anion, hydroxyl radical) and RNS (e.g., nitric oxide or NO) have important signaling functions in plants. These can be observed via the interaction of ROS and NO to form a range of RNS, apart from both being able to modify proteins involved in NO and ROS metabolism, signaling, and homeostasis <sup>[6]</sup>. However, the accumulation of ROS and RNS buildup may result in cellular damage and inactivation of important signaling molecules; therefore, proper regulation of ROS/RNS homeostasis forms an important feature of abiotic stress tolerance and resistance <sup>[3][7]</sup>.

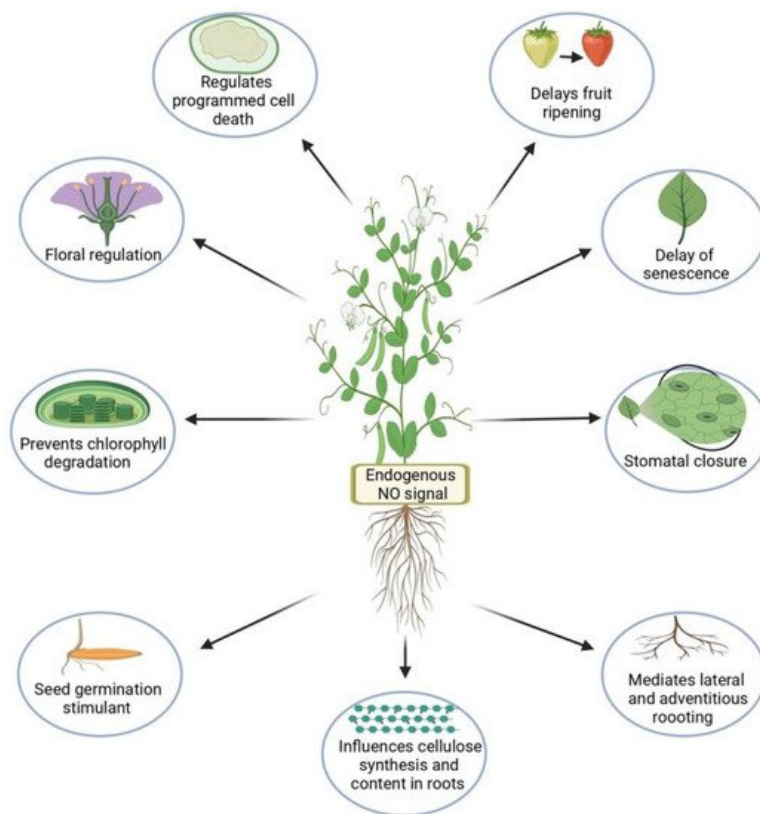
Depending on their concentration, both NO and ROS act as double-edged swords. NO, an extremely reactive free radical and weak oxidant, is a unique type of diffusible signaling molecule first identified as an endothelium-derived relaxing factor <sup>[8]</sup>. Since then, it has been found to be involved in various physiological processes in mammals, such as neurotransmission, vasodilation, immune regulation, inhibition of platelet aggregation, apoptosis, and defense against microbes <sup>[9][10][11][12][13]</sup>. However, the emission of NO was first observed in plants by Klepper in Glycine max plants treated with herbicides, earlier than in animals <sup>[14]</sup>. NO is biologically active at 1 nmol/L concentration and participates in various signaling pathways to regulate plant growth and development <sup>[15]</sup>. In most of the experimental studies ([Table 1](#) and [Table 2](#)), a 100  $\mu$ M aqueous SNP (NO donor) solution has been shown as the best dose, with some studies showing 200 as well, releasing nanomolar amounts of NO. In plants, it is involved in the regulation of a number of physiological processes, such as stomatal movement ([Figure 1](#)) <sup>[16]</sup>, photosynthesis <sup>[17]</sup>, induction of apoptosis <sup>[18]</sup>, senescence <sup>[19]</sup>, floral regulation <sup>[20]</sup>, seed germination <sup>[21]</sup>, lateral root formation <sup>[22]</sup>, adventitious root formation <sup>[23]</sup>, regulation of cellulose content in roots ([Figure 2](#)) <sup>[24]</sup>, and various responses to abiotic and biotic stresses, sometimes in interaction with other hormones <sup>[12][25][26]</sup>. It also plays an important role in regulating toxicity and levels of ROS ([Figure 1](#)), which is important for cytoprotection <sup>[27]</sup>. Because of its versatility and biological importance, it was rightly named “Molecule of the Year” by Science in 1992 <sup>[28]</sup>.

ROS are produced as unwanted byproducts of various metabolic pathways in chloroplasts, mitochondria, peroxisomes, and legume nodules <sup>[29][30][31][32]</sup>. Their production is also induced by various abiotic and biotic stresses to regulate different processes, such as programmed cell death, pathogen defense, and stomatal behavior <sup>[5][33]</sup> as well as other signaling pathways that modulate plant functions <sup>[2]</sup>. When produced in excess and depending on the concentration and site of production, ROS can also oxidize and alter cellular components, modify proteins and lipids, and irreversibly

damage DNA [34][35]. Therefore, plants require an appropriate homeostatic mechanism to maintain ROS levels within thresholds through various ROS interception systems to maximize their beneficial effects and minimize their cytotoxic effects on plants [31][36] (Figure 1).



**Figure 1.** Schematic diagram showing the functional roles played by nitric oxide (NO) in plants exposed to drought, heavy metal, and salinity stress. NO enhances the activity of  $\text{Na}^+/\text{H}^+$  antiporters on the vacuole membrane as well as the plasma membrane, such as SOS1, which helps in the removal of excess  $\text{Na}^+$  from cell cytoplasm. It also facilitates  $\text{K}^+$  ion entry into cells to maintain a balanced  $\text{Na}^+/\text{K}^+$  ratio during salinity stress. NO up-regulates the activity of antioxidant enzymes, thiols, and compatible osmolytes, which protect the plants against salinity, drought, and HM stress by preventing membrane damage, ion and metal toxicity, osmotic stress, lipid peroxidation, and excess ROS production. It is involved in phytochelatin (PC) biosynthesis via GSH with the help of enzymes PCS; these PCs then help in sequestration of excess metals. NO also increases cytosolic free  $\text{Ca}^{2+}$  through cGMP and cADPR up-regulation. High cytosolic  $\text{Ca}^{2+}$  causes stomatal closure due to the activation of outward anion channels such as SLAC1 and inhibition of  $\text{K}^+$  inward channels. This helps in optimizing water usage during drought stress. Pro: Proline; GSH: Glutathione; GB: Glycine betaine; PCS: Phytochelatin synthase; HM-PC: Heavy metal-Phytochelatin complex; cADPR: Cyclic ADP-Ribose; cGMP: Cyclic GMP; CAT: Catalase; SOD: Superoxide dismutase; GR: Glutathione reductase; GST: Glutathione S-transferase; APX: Ascorbate peroxidase; IP3: Inositol triphosphate (it acts as a second messenger); Cyt: Cytosolic. Made with Biorender.com (Accessed on 3 September 2021).



**Figure 2.** Role of NO in plant growth and development. (Made with [Biorender.com](https://biorender.com) (accessed on 3 September 2021)).

**Table 1.** Compilation of recent research studies investigating the role of NO in ameliorating drought stress in plants.

Plant Species	Drought Imposition	Concentration and Source of NO	Plant Response to NO	Reference
<i>Citrullus lanatus</i> (watermelon)	15% PEG 600	100 $\mu$ M SNP	Reduction in MDA content Increased activity of APX Reduced oxidative damage Increased proline content	[37]
<i>Glycine max</i>	Withholding water	100 $\mu$ M SNP	Reduced water loss and improved biomass due to alteration of stomatal characteristics and hydraulic conductivity	[38]
<i>Origanum majorana</i>	Withholding water	30 and 60 $\mu$ M SNP	Improved water use efficiency Increased anthocyanin, soluble phenol, and flavonoid content Enhanced antioxidant capacity	[39]
<i>Brassica juncea</i>	10% PEG 6000	100 $\mu$ M SNP	Antioxidant accumulation Reduction in MDA content Decreased ROS content	[40]
<i>Triticum aestivum</i>	15 and 30% PEG	0.5 mM SNP	Improved antioxidant defence Enhanced glyoxalase system resulting in restoration of leaf relative water content and proline content Enhanced endogenous NO production	[41]
<i>Zea mays</i>	Withholding water	50, 100, 150, and 200 $\mu$ M SNP	100 $\mu$ M SNP had a positive impact on chlorophyll content and water status Increased activity of CAT, SOD, and APX Improved activities of GR, GST, GOPX, nitrite and nitrate reductase activity	[42]

PEG: Polyethylene glycol; NO: Nitric oxide; SNP (Sodium nitroprusside); acts as NO donor; MDA: Malondialdehyde; APX: Ascorbate peroxidase; ROS: Reactive oxygen species; CAT: Catalase; SOD: Superoxide dismutase; GR: Glutathione reductase; GST: Glutathione S-transferase; GOPX: Guaiacol peroxidase.

**Table 2.** Compilation of recent studies on the effects of exogenous NO application on plants under heavy metal stress.

Table	Source and Concentration of Metal	Source and Concentration of Exogenous NO	Plant Species	Impact of NO Treatment	Reference
A: Copper	200, 400 $\mu\text{M}$ $\text{CuSO}_4$	200, 300 $\mu\text{M}$ SNP	<i>Lactuca sativa</i>	Decreased DNA methylation Decreased genomic template instability Increased POX and SOD activity	[43]
	5, 25, 50 $\mu\text{M}$ $\text{CuSO}_4$	10 $\mu\text{M}$ SNP	<i>Arabidopsis thaliana</i>	Increased cell viability	[44]
	200 $\mu\text{M}$ $\text{CuCl}_2$	100 $\mu\text{M}$ SNP	<i>Lolium perenne</i>	Increased activity of SOD, CAT, APX and POX Increased chlorophyll content and photosynthesis Maintenance of Ion homeostasis	[45]
	0.2 mM Cu	0.05 mM SNP	<i>Nicotiana tabacum</i>	Increased chlorophyll content, RUBISCO activity and fresh weight	[46]
	450 $\mu\text{M}$ $\text{CuSO}_4$	200 $\mu\text{M}$ SNP	<i>Hordeum vulgare</i>	Enhanced antioxidant enzyme activity and reduced lipid peroxidation Activation of AsA-GSH cycle	[47]
	150 $\mu\text{M}$ Cd	150 $\mu\text{M}$ SNP	<i>Hordeum vulgare</i>	Decreased $\text{H}_2\text{O}_2$ and $\text{O}_2^-$ contents Increased AsA, and GSH content Increased expression of HvAOX1a gene	[48]
B: Cadmium	200 $\mu\text{M}$ $\text{CdSO}_4$	200 $\mu\text{M}$ SNP	<i>Catharanthus roseus</i>	Increased melatonin and endogenous NO concentration Increased activities of CAT, SOD, POX Decreased $\text{H}_2\text{O}_2$ and lipid peroxidation in roots	[49]
	100 $\mu\text{M}$ $\text{CdSO}_4$	50 $\mu\text{M}$ SNP	<i>Oryza sativa</i>	Decreased Cd uptake by roots Restores RNS/ROS balance	[50]
	5, 7, or 9 $\mu\text{M}$ $\text{CdCl}_2$	300 $\mu\text{M}$ SNP	<i>Vigna radiata</i>	Improvement adventitious formation in hypocotyl cuttings Prevents lipid peroxidation Enhanced antioxidant enzyme activity	[51]
	150 $\mu\text{M}$	100 $\mu\text{M}$ SNP	<i>Solanum lycopersicum</i>	Reduced Cd uptake Enhanced AsA-GSH cycle Increased activities of SOD, CAT, GR, MDHAR and APX	[52]

Table	Source and Concentration of Metal	Source and Concentration of Exogenous NO	Plant Species	Impact of NO Treatment	Reference
C: Arsenic	75 mg/kg (NaAsO <sub>2</sub> )	100 µM SNP	Brassica juncea	Increased activities of antioxidant enzymes Increased thiol and proline biosynthesis Decreased As uptake	[53]
	50 µM (Sodium arsenate)	100 µM SNP	Brassica seedlings	Recovery of photosynthetic pigments Increased CAT and SOD activity resulting in decreased H <sub>2</sub> O <sub>2</sub> and Recovery of AsA and GSH content	[54]
	150 µM (Sodium meta arsenite)	100 µM SNP	Oryza sativa	Enhanced nitrogen and thiol content Improved nitrate reductase and GOGAT activity Improved amino acid content	[55]
	1.5 mg L <sup>-1</sup> As	0.1 mg L <sup>-1</sup> SNP	Pistia stratiotes Leaves	Reduced ROS content Improved photochemical efficiency of PSII Maintained the integrity of cell organelles	[56]
	500 µM ZnSO <sub>4</sub> ·7H <sub>2</sub> O	100 µM SNP	Carthamus tinctorius	Reduced Zn translocation from root to shoot Enhanced activity of AsA-GSH cycle and glyoxalase system enzymes	[57]
D: Zinc	100, 200 µM ZnO nanoparticles	100 µM SNP	Triticum aestivum	Decreased Zn accumulation in xylem and phloem saps Improved activity of AsA-GSH cycle	[58]
	0.05, 0.5 mM Zn (zinc sulfate) in nutrient solution	0.1 mM SNP	Zea mays	Increased chlorophyll content Decreased leaf and root Zn content Increased nitrogen and iron content	[59]

## 2. Nitric Oxide (NO) Signaling under Abiotic Stresses

### 2.1. NO and Drought Stress

There is credible evidence that NO functions as a vital signaling molecule during both normal growth and development, and drought stress; exogenous application of NO mitigates the negative effects of drought, as seen in soybean, cucumber, and many other plants [38][60][61]. NO has been shown to mediate drought tolerance by activating the ROS scavenging enzyme system [62] and increasing osmolyte and proline metabolism [63]. NO also modulates water loss through abscisic acid-mediated stomatal response by acting as a secondary messenger in various signaling pathways, such as cyclic guanosine monophosphate (cGMP), mitogen-activated protein kinase (MAPK), and Ca<sup>2+</sup> pathways [64].

#### 2.1.1. NO and ROS-Mediated Oxidative Stress

During drought stress, plants produce excessive amounts of ROS (oxidative burst) due to a decrease in photosynthesis, leading to an excessive reduction in the electron transport chain and subsequent photooxidative stress [65]. NO mitigates the deleterious effects of ROS by limiting lipid peroxidation, increasing the rate of photosynthesis, and promoting antioxidants through various signaling pathways, e.g., the MAP kinase pathway [66][67]. Drought tolerance of plants is significantly enhanced by the activation of antioxidant enzyme systems such as CAT, SOD, GOPX, APX, DHAR, and GR [68]. The activity of CAT and SOD is down-regulated under drought, while application of NO up-regulates antioxidant activity as seen in hull-less barley [69]. The metalloenzyme SOD catalyzes the dismutation of superoxide to form H<sub>2</sub>O<sub>2</sub>, which is then converted to H<sub>2</sub>O and O<sub>2</sub> by CAT and POX [70]. Activation of different isoforms of SOD under drought is considered as a strategy to counteract superoxide anion (O<sub>2</sub><sup>-</sup>) accumulation in different cellular compartments [71][72]. SOD is quite important in preventing the reaction of O<sub>2</sub><sup>-</sup> with proteins, with unsaturated fatty acids for peroxidation, or with

NO to form ONOO<sup>-</sup>; thus, transgenic plants overexpressing Cu or Zn isoforms of the SOD gene from *Puccinellia tenuiflora* have increased drought tolerance [73]. Fan et al. [74] showed that treatment with the NO donor, i.e., sodium nitroprusside (SNP), under drought, up-regulated the activities of SOD, CAT, and POX, resulting in lower ROS accumulation in such plants (Table 1). Increased malondialdehyde (MDA) content and electrolyte loss are important indicators of oxidative damage to cell membranes [75], and application of NO can counteract the negative effects of drought by reducing electrolyte loss and decreasing leaf H<sub>2</sub>O<sub>2</sub> and MDA content [69]. NO generation has been reported to be up-regulated in *Cucumis sativus* seedlings upon polyamine (spermine and spermidine) treatment, and its exogenous application in the form of SNP counteracts lipid peroxidation and membrane damage induced by drought stress [8]. Moreover, they also found that exogenous NO application had no effect on endogenous polyamine levels in plants under drought stress but were positively correlated with mitigation of drought induced damage, indicating that polyamines act up-stream of NO in drought stress response.

### 2.1.2. NO and Stomatal Closure during Drought

The exact mechanistic role of NO in ABA-mediated stomatal closure is not yet clear, but it has been proposed that NO is an important component of the ABA signaling pathway for stomatal closure [76]. NO acts downstream of the ABA signaling pathway and is an important component of the drought signaling network involved in the control of stomatal transpiration [38][60]. In a study conducted by Van Meeteren [77] on leaves of *Vicia faba* using SNP, NO gas, and ABA, they concluded that NO modifies stomatal opening through several pathways but is probably not critical for rapid ABA-induced stomatal closure. They found that NO/SNP application did not induce stomatal closure in epidermal cells, contradicting previous studies, whereas ABA application did induce stomatal closure [77].

### 2.1.3. NO and Drought-Responsive Genes

Transcription factors are important molecular players that bind to gene promoters to activate or repress transcription. Interestingly, a number of transcription factors are NO-responsive and drought-dependent [78][79]. Overexpression of SIWRKY8, which belongs to the WRKY transcription factor superfamily, increases drought tolerance in tomato [80]. In contrast, SIWRKY81 negatively regulates tomato drought tolerance by repressing NR activity, leading to reduced NO accumulation and eventually to reduced stomatal closure, which in turn increases water loss [81]. Silencing of SIWRKY81 resulted in increased NO accumulation in guard cells due to increased NR expression, leading to more efficient stomatal closure and reduced water loss [81]. Thus, silencing of SIWRKY81 can be used to increase tolerance in many drought-sensitive plants. Research on NO-mediated gene regulation in plants under drought stress is limited, and further research is needed to fully elucidate its role and paint a more comprehensive mechanistic picture.

## 2.2. NO and Metal/Metalloid Stress

Naturally occurring metallic elements with relatively higher atomic weight and density than water are called heavy metals (HMs) [82]. Contamination of the environment with HMs mostly occurs through anthropogenic activities, such as the use of metals and metal-containing compounds in agriculture and households, mining and smelting, and industrial production [20][83].

One of the main consequences of HM stress in plants is the excessive ROS formation, due to Fenton and Haber–Weiss reactions and changes in the antioxidant system [84][85]. Certain metals such as lead and cadmium (Cd) are not directly involved in ROS formation, but they inhibit the antioxidant system and divert electrons from the electron transport chain, indirectly promoting ROS formation [86][87]. Both endogenous and exogenous NO may play a role in plant perception, signaling, and stress acclimation under HM stress [88]. NO is readily diffusible across membranes and is involved in the regulation of numerous physiological processes, including responses to HM stress [89].

### 2.2.1. Cadmium Stress

Cadmium (Cd), a non-essential element and one of the most hazardous pollutants, can be toxic to animals even at non-phytotoxic concentrations [90]. It is rapidly taken up by plants due to its high mobility through Fe<sup>2+</sup>, Ca<sup>2+</sup>, Zn<sup>2+</sup>, and Mn<sup>2+</sup> transporters, such as the ZIP IRT1 transporter [91]. As reviewed by Terrón-Camero et al. [89], NO donor application correlates negatively with HM uptake, except for Cd, which showed a positive correlation in about 40% of the studies. Cd accumulation in response to NO could most likely be due to stimulation of IRT1, which has been shown to be NO-dependent and inhibited in the presence of NO synthase inhibitor [92][93][94]. Sharing of IRT1 transporters under Cd stress leads to iron deficiency, which in turn results in NO-mediated up-regulation of FRO2 (Ferric reduction oxidase 2), IRT1 (Iron-regulated transporter 1), and FIT (FER-Like Fe deficiency induced transcription factor), leading to additional Cd accumulation [92]. Cd stress has been reported to induce endogenous NO generation, which reduces root growth due to shortening of the root elongation zone, an effect that is reversed by the NOS inhibitor L- NAME (N omega-Nitro-L-arginine methyl ester hydrochloride) [77]. However, exogenous NO may prevent the reduction of root growth in response to HM

stress [77]. NO accumulation under Cd stress leads to the inhibition of root meristem in Arabidopsis due to the reduced AUX level in roots, and this inhibition was alleviated by the application of NO scavengers such as L- NAME and cPTIO (2-4-carboxyphenyl-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide) [95]. These results suggest that NO has a negative effect on root growth and development under Cd stress. Moreover, the application of NO mitigates the negative effects of Cd stress on plant growth and development [52][96].

### 2.2.2. Copper Stress

Cu application has been reported to induce the formation of NO, which is mainly attributed to NOS, one of the most important enzymes in the production of NO [97]. However, Hu et al. [47] reported that early NO production in *Hordeum vulgare* under Cu stress was instead due to the activity of NR (not NOS), as the use of NR inhibitors resulted in decreased NO production in such plants. NO-mediated attenuation of Cu stress could be due to the up-regulation of defense-related genes or antioxidant enzyme activity [98]. In addition, NO also maintains the balance of cellular free metal concentrations by controlling their accumulation or excluding HMs in roots [98]. Application of SNP to *B. juncea* seeds increased their germination rate and alleviated Cu-induced oxidative stress due to enhancement of the antioxidant system, including SOD, GR, and APX, thereby lowering lipid peroxidation and H<sub>2</sub>O<sub>2</sub> levels [99].

### 2.2.3. Arsenic Stress

Arsenic (As) is a highly toxic metalloid whose toxicity causes various symptoms such as necrosis, decreased photosynthesis, and growth inhibition [87]. First, it causes an increase in ROS, leading to increased lipid peroxidation and protein carboxylation, which negatively affect metabolism and disrupt cellular ultrastructure [100]. Arsenic also inhibits the activity of enzymes by binding to their sulfhydryl groups (-SH), thereby hindering several important cellular functions [101]. Souri et al. [102] suggested that As tolerance of *Isatis capadoccica* (an As hyperaccumulator) may be related to NO as SNP treatment enhances plant growth under As stress, while the application of an NO scavenger and the NOS inhibitor L-NAME reduces plant growth. They concluded that SNP treatment correlated with increased proline, GSH, thiol, and antioxidant concentrations, such as CAT, APX, SOD, and GR, which prevent lipid peroxidation and H<sub>2</sub>O<sub>2</sub> accumulation. GSH, an important thiol compound, is also involved in As tolerance by participating in the biosynthesis of phytochelatin (metal-binding peptide), which binds As III, preventing its toxicity [102]. This phytochelatin complex formation is regulated by NO and is considered to be one of the major mechanistic reasons for As hypertolerance in *I. capadoccica* [103]. The application of SNP to rice plants under As stress can increase primary root length and number of lateral roots compared to As alone, indicating the role of NO in mitigating the effects of As stress on root development [104].

### 2.2.4. Zinc Stress

Accumulation of zinc (Zn) in the environment occurs through both natural causes (volcanic eruptions, fires, and weathering) and anthropogenic activities (electroplating, mining, ore processing, ink and battery industries, and agrochemical application) [105][106]. Zn plays an important role in various redox reactions and is an essential cofactor of several enzymes, such as SOD, when present in the homeostatic range [107]. It is required by plants in trace amounts and is involved in several enzyme-catalyzed reactions; therefore, its toxicity impairs these reactions, which in turn can lead to oxidative stress, senescence, and retarded growth [108]. As reported by Kolbert et al. [109], Zn stress in Arabidopsis leads to reduced activities of CAT and APX and decreased GSH content, resulting in an overall excess of H<sub>2</sub>O<sub>2</sub>.

### 2.2.5. Other Heavy Metal Stresses (Lead, Chromium, Mercury)

Lead (Pb) is one of the most important environmental pollutants, especially in regions with high anthropogenic activities [110], and in toxic concentrations it negatively affects crop biomass as well as yield [111]. At high concentrations, it leads to reduced growth, ROS accumulation, irregular phytomorphology, and cell death [112]. As reported by Okant and Kaya [113], Pb stress leads to increased NO content in maize leaves, and this has also been reported for other plants in previous studies involving different HMs [114].

Due to extensive industrial use, chromium (Cr) contamination has become a cause of environmental and scientific concern, with hexavalent Cr(VI) considered the most toxic among its various oxidation states [115]. Since it is not an essential element, there is no specific mechanism for its uptake and it competes with sulphur, phosphorus, and iron in carrier binding [116]. Once it enters the plants, it causes adverse effects in the plants from molecular level to whole plant level. Huang et al. [117] found that NO has the potential to attenuate Cr(VI) toxicity in tall fescue plants, improve the performance of the pigment system II, and improve overall physiological properties in these plants. NO has also been found to be helpful in mitigating Cr(VI) disadvantages in maize seedlings by suppressing lipoxygenase activity and enhancing antioxidant enzyme activities [118]. NO has been found to play a crucial role in germination and seedling development under Cr stress. Under Cr(VI) stress, the application of SNP improves seed germination and seedling

development of tomato and increases the activity of protease and  $\alpha$ -amylase hydrolyzing enzymes [119]. Furthermore, they reported an increase in nitrogen, proline, thiol content and antioxidants. These results suggest that exogenous NO application could be useful in Cr phytoremediation.

Mercury (Hg) is a non-essential element and contamination has become a major ecological problem due to the continuous release of Hg into ecological systems due to anthropogenic activities. Hg is introduced into agricultural soils through the use of Hg-containing compounds such as pesticides, fertilizers, lime, and soil amendments, resulting in Hg contamination [120]. Among the various forms of Hg,  $Hg^{2+}$  is the predominant and bioavailable form to plants [121]. The application of SNP showed positive correlation in attenuating the adverse effects of Hg toxicity in three soybean cultivars (Pusa-24, Pusa-37, and Pusa-40), where Pusa-37 showed better response to NO under Hg stress compared to the other cultivars [122]. They reported an increase in antioxidant response and the AsA-GSH cycle after SNP treatment in these plants. Chen et al. [123] reported that exogenous NO treatment attenuated Hg toxicity (in the form of  $HgCl_2$ ) in rice seedlings by preventing oxidative stress in leaves and promoting auxin transport in roots. They also reported a decrease in Hg absorption and transport and reduced ROS content.

### 2.3. NO and Salinity Stress

The role of NO in salt tolerance has been studied in several plant species, and there is ample evidence that application of NO donor protects plants from salt stress by protecting against oxidative stress, maintaining ion homeostasis, regulating osmolyte accumulation, and improving physiological and biochemical parameters [124][125][126]. Treatment of pepper seedlings with 150 mM NaCl resulted in an increase in MDA and  $H_2O_2$  content by ~100% and 87%, respectively, compared to the control [127]. However, they found that foliar application of 150  $\mu$ M SNP to such seedlings decreased MDA and  $H_2O_2$  content to 54% and 34%, respectively; it also improved leaf relative water content and antioxidant enzyme activity (SOD, POX, CAT) [127]. Ren et al. [126] reported that NO (10  $\mu$ M SNP) pretreatment attenuated the inhibition of seed germination and early seedling growth of *Brassica chinensis* under salt stress. They found that SNP pretreatment increased antioxidant enzyme activity such as CAT, APX, and SOD and reduced  $H_2O_2$  and MDA content, which reduced NaCl-induced oxidative damage. They also reported an increase in soluble sugar and proline content and increased  $K^+/Na^+$  ratio in Radicula and Plumula. The maintenance of high  $K^+/Na^+$  ratio and reduced  $Na^+$  accumulation is important for salt tolerance in plants as they reduce ion toxicity and contribute to the restoration of various metabolic processes [128]. The increased  $K^+/Na^+$  ratio and decreased  $Na^+$  accumulation in NO-treated seedlings under salt stress is likely due to the inhibition of vacuolar  $Na^+$  compartmentation or  $Na^+$  influx through the plasma membrane of radicle [129]. Moreover, the increased  $K^+$  content and  $K^+/Na^+$  ratio in NO-treated plants under salt stress could be due to decreased  $K^+$  efflux, an increase in competitive absorption sites, increased SOS1 transporter activity, and reduced  $H_2O_2$  content [128][130]. In addition, NO was also able to induce the expression of  $H^+$ -PPase and  $H^+$ -ATPase, which detoxify the cell through  $Na^+/H^+$  exchange, as well as the expression of AKT1-type  $K^+$  channels, ultimately leading to increased salinity tolerance [131]. NO assists sunflower seedlings to adapt to salinity stress (120 Mm NaCl) by regulating polyamine homeostasis by increasing the accumulation of polyamine biosynthetic enzymes, decreasing polyamine catabolism, and regulating their distribution [132]. Consistent with this, foliar application as well as pretreatment of NO also alleviates salinity-induced stress in broccoli plants by increasing antioxidant enzyme activity, decreasing MDA and  $H_2O_2$  content, and improving glycine betaine, phenolics, and chlorophyll-a content [133]. NO acts as a cellular preservative that induces the expression of various genes controlling metabolic processes and also alters ROS content [12][134] (Table 3).

**Table 3.** Compilation of recent studies on the role of NO in ameliorating plant responses to salinity stress.

Experimental Plant	NaCl Concentration	Concentration and Source of NO	Impact of NO on Plants	Reference
<b>Jatropha curcas</b>	<b>100 mM</b>	<b>75 <math>\mu</math>M SNP</b>	<b>Reduced oxidative damage</b> <b>Decreased toxic ion and ROS accumulation</b> <b>Increased accumulation of AsA and GSH</b> <b>Increased activity of CAT, SOD and GR</b>	[134]
<b>Brassica oleracea (Broccoli)</b>	<b>120 mM</b>	<b>0.02 mM SNP</b>	<b>Improved CAT, SOD, and POX activity</b> <b>Increased glycine betaine and total phenolic content</b> <b>Reduction in <math>H_2O_2</math> and MDA content</b>	[133]



Experimental Plant	NaCl Concentration	Concentration and Source of NO	Impact of NO on Plants	Reference
<b>Crocus sativus (Saffron)</b>	<b>50 and 100 mM NaCl</b>	<b>10 <math>\mu</math>M SNP</b>	<b>Improved growth Accumulation of compatible solutes Increased antioxidant enzyme activity and secondary metabolite biosynthesis</b>	<b>[135]</b>
<b>Hylotelephium erythrostictum</b>	<b>200 mM NaCl</b>	<b>50 <math>\mu</math>M SNP</b>	<b>Increased Na<sup>+</sup> efflux and decreased K<sup>+</sup> efflux Increased Ca<sup>2+</sup> influx</b>	<b>[136]</b>
<b>Brassica napus (Rapeseed)</b>	<b>200 mM NaCl</b>	<b>10 <math>\mu</math>M SNP</b>	<b>Redox and ion homeostasis Modulation of antioxidant defence genes SOS2 and NHX1</b>	<b>[137]</b>
<b>Cicer arietinum L. (chickpea)</b>	<b>50 and 100 mM NaCl</b>	<b>50 <math>\mu</math>M SNAP (S-nitroso-N-acetylpenicillamine)</b>	<b>Increased osmolyte accumulation Upregulation of CAT, SOD and APX genes Decreased electrolyte leakage, MDA and H2O2 content</b>	<b>[125]</b>
<b>Gossypium (Cotton) seedlings</b>	<b>100 mM NaCl</b>	<b>0.1 and 1.00 mM SNP</b>	<b>Increased K<sup>+</sup> Decreased K<sup>+</sup>/Na<sup>+</sup> ratio Increased antioxidant enzyme activity Decreased MDA content</b>	<b>[138]</b>

SNP and SNAP are NO donors.

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