



Involvement of nitric oxide (NO) in plant responses to metalloids

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ABSTRACT

Plants respond to the limited or excess supply of metalloids, boron (B), silicon (Si), selenium (Se), arsenic (As), and antimony (Sb) via complex signaling pathways that are mainly regulated by nitric oxide (NO). The absorption of metalloids from the soil is facilitated by pathways that involve aquaporins, aquaglyceroporins, phosphate, and sulfate transporters; however, their regulation by NO is poorly understood. Using *in silico* software, we predicted the S-nitrosation of known metalloid transporters, proposing NO-dependent regulation of metalloid transport systems at the posttranslational level. NO intensifies the stress-mitigating effect of Si, whereas in the case of Se, As, and Sb, the accumulation of NO or reactive nitrogen species contributes to toxicity. NO promotes the beneficial effect of low Se concentrations and mitigates the damage caused by B deficiency. In addition, the exogenous application of NO donor, sodium nitroprusside, reduces B, Se, and As toxicity. The primary role of NO in metalloid stress response is to mitigate oxidative stress by activating antioxidant defense at the level of protein activity and gene expression. This review discusses the role of NO in plant responses to metalloids and suggests future research directions.

1. Introduction

The diverse group of metalloids includes boron (B), silicon (Si), arsenic (As), selenium (Se), antimony (Sb), germanium (Ge), tellurium (Te), and polonium (Po). While most metalloids are non-essential to land plants, metalloids such as As, Ge, and Sb are hazardous to plants and harmful to human health. However, B is an exception; it is an essential nutrient primarily because it stabilizes the cell wall matrix by cross-linking with the cell wall component rhamnogalacturonan II (O'Neill et al., 1996). B also positively influences plant reproductive development, seed quality, and antioxidant and polyphenol synthesis. Moreover, it is involved in the nucleic acid synthesis, phenol metabolism, and carbohydrate biosynthesis (Landi et al., 2019).

Recently, Lewis (2019) questioned the essential role of B in plants, arguing that the formation of B complexes in the cell wall is a detoxifying mechanism rather than the evidence of its essentiality. As a result, a scientific debate occurred (Wimmer et al., 2020; González-Fontes,

2020; Lewis, 2020). Excess B has been proven to cause growth impairment, necrosis in leaves and stems, and malformation of fruits as well as altered root growth (Landi et al., 2019). Si is recognized as a semi-essential element because in its absence, plants develop without symptoms. However, in silicified species, such as horsetail and rice, Si deficiency increases susceptibility to fungal infection (Law and Exley, 2011). In addition, Si added to the growth medium enhances plant fitness and resistance to (a)biotic stress (Azeem et al., 2015; Coskun et al., 2016; Guerriero et al., 2016) by, among other things, promoting efficient water use, activating defense enzymes and metabolites, and delaying senescence (Frew et al., 2018). In the plant kingdom, Se, like Si, is essential for algae but not for higher plants. This indicates that the capability of using Se as an essential nutrient has been evolutionarily lost (Pilon-Smits and Quinn, 2010; Schiavon and Pilon-Smits, 2017). At low concentrations, Se exerts positive effects on germination as well as vegetative and reproductive growth, delays senescence, and alleviates abiotic stresses (Kolbert et al., 2019a). Unlike Si, Se exerts a phytotoxic

Abbreviations: Al, Aluminum; Sb, antimony; As, arsenic; AsA, ascorbate; APX, ascorbate peroxidase; B, boron; Cd, cadmium; cPTIO, 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide; CAT, catalase; CK, cytokinin; DHAR, dehydroascorbate reductase; ET, ethylene; GSH, glutathione; GPX, glutathione peroxidase; GST, glutathione-S-transferase; Hb, hemoglobin; H₂O₂, hydrogen peroxide; H₂S, hydrogen sulfide; *OH, hydroxyl radical; LPO, lipid peroxidation; MDHAR, monodehydroascorbate reductase; NR, nitrate reductase; L-NMMA, N^G-monomethyl-L-arginine; NO, nitric oxide; NOS, nitric oxide synthase; L-NAME, N^ω-Nitro-L-arginine methyl ester; ONOO⁻, peroxynitrite; POD, peroxidase; PGPR, plant growth promoting rhizobacteria; P5CS, pyrroline-5-carboxylate synthase; RNS, reactive nitrogen species; ROS, reactive oxygen species; SA, salicylic acid; Se, selenium; SeCys, selenocysteine; SeMet, selenomethionine; Si, silicon; GSNO, S-nitrosoglutathione; GSNOR, S-nitrosoglutathione reductase; SNO, S-nitrosothiol; SNP, sodium nitroprusside; O₂⁻, superoxide anion; SOD, superoxide dismutase.

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Table 1

The metalloid transporter proteins predicted to be modified by S-nitrosation. The amino acid sequences in the FASTA format were downloaded from the UniProt database and uploaded to the GPS-SNO 1.0 and iSNO-PseAAC software. The predictions were performed using a medium threshold. The prediction results on the positions and peptides were extracted into an Excel file for further analysis. The target Cys (C) are indicated in italics, and Cys predicted by both computational tools are labeled with asterisks.

Transporter	Metalloid transported	GPS-SNO 1.0		iSNO-PseAAC	
		Cys position of S-nitrosation	Amino acid sequence	Cys position of S-nitrosation	Amino acid sequence
ZmPIP1-1	B(OH) ₃	141*	TRAVFYIIMQCLGAICGRGVV	141*	TRAVFYIIMQCLGAICGRGVV
ZmPIP1-2	B(OH) ₃	143	LFYIIMQCLGAVCGA	n.d.	
AtNIP5;1	B(OH) ₃ , As(III)	n.d.		116	GAETLIGNAACAGLAVMIIL
				168	YIAAQVSASICASFALKGVFH
AtNIP6;1	B(OH) ₃ , As(III)	n.d.		115	KTDGAETLIGCAASAGLAVMI
HvPIP1;3	B(OH) ₃	146*	VFYIVMQLGAICGA	146*	TRAVFYIVMQLGAICGAGVV
HvPIP1;4	B(OH) ₃	146*	VFYIVMQLGAICGA	146*	VFYIVMQLGAICGA
AtBOR1	B(OH) ₃	78	TLASTAICGMIHSII	129	DLFLAWSGWVVCVWTALMLFVL
				145	MLFLVAICGACSIIINRFTRVA
				477	NLLQSTMVGGCVAAMPILKMI
				557	TLFQTTYLLICFGLTWIPIAG
AtBOR2	B(OH) ₃	78*	TLASTAICGIIHSII	78*	AVQTLASTAICGIIHSIIGGQ
		627	GSTASYPDCSEILDE	129	NLFLAWSGWVVCVWTSLILFVL
		647*	RGEFRHTCSPKVTSS	477	NLLQAVMVGVCVAAMPPLKMI
				647*	TRSRGEFRHTCSPKVTSSST
OsLsi1 (OsNIP2;1)	Si, Se(IV)	204	LAVGSAVCITSIFAG	139	YWAAQFTGAICASFVLKAVIH
OsLsi2	Si	123	ALFTNDTCCVVLTEF	108	QGGRDLMCRVCVVTALASALF
		317	DFRDAEPCLDTVSYS	124	ASALFTNDTCCVVLTEFVLEL
				265	ITTKHPWFMCTEARRKFLK
HvLsi1	Si	66*	FLLVFVTCGAAAISA	66*	VSTFLLVFVTCGAAAISAHDV
		204	LAVGSSVCITSIFAG	139	YWAAQFTGAICASFVLKAVLH
ZmLsi1	Si	202	LAVGSAVCITSIFAG	n.d.	
ZmLsi6	Si	n.d.		n.d.	
AtSULTR1;2	Se(VI), SO ₄ ⁻²	135	VPPLVYACMGSSRDI	469	FKVDKLDFIACIGAFFGVIFV
		406	AVNFMAGCQTAVSNI		
		645	VADAVEACCPKLSNE		
AtSULTR2	Se(VI), SO ₄ ⁻²	431	AVNFAAGCETAMSNI	56	QPDRSKWLLDCPEPPSPWHEL
		450*	TVFVALECLTRLLYY	450*	MAVTVFVALECLTRLLYYTPI
		568*	RVKSALLCFANASSI	568*	LIFRVKSALLCFANASSIEER
				672	YLTIGEALDACFGLKVXXXXX
AtPHT1;1	As(V)	n.d.		41	GFFTDAYDLFCVSLVTKLLGR
				111	YGLTLMVMILCSVASGLSFGH
				131	HEAKGVMTTLCFRFRWLGFGI
AtPHT1;4	As(V)	111*	TLMVMVLCIASGLS	41	GFFTDAYDLFCISLVTKLLGR
				111*	YGMTLMVMVLCIASGLSFGH
				131	HEPKAVMATLCFRFRWLGFGI
AtPHT1;7	As(V)	111*	TLMVMVLCIASGLS	41	GFFTDAYDLFCISLVTKLLGR
				111*	YGMTLMVMVLCIASGLSFGS
				131	SNPKVTMTLCFRFRWLGFGI
AtPHT1;8	As(V)	117	VCTTRRSCVMVSLGF	38	GLFTDAYDLFCIAPVMKMISH
				95	RVGRRRVYGLCLIHILSSFG
				179	LVSSAVTMAVCVAFKRSGGGL
				482	RIAFLLGGVCIAGILVYTF
AtPHT1;9	As(V)	118	VCTTRRSCVMVSLGF	39	GLFTDAYDLFCIAPIMKMISQ
				180	LMSSAVTMVVCLAFKNAGEGS
				488	RIAFLLGGVCIAGMIVTYLF
OsPHT1;1	As(V)	n.d.		41	GFFTDAYDLFCISLVTKLLGR
				111	YGFLLLMVVCVSVASGLSFGS
				131	SSAKGVVSTLCFRFRWLGFGI
OsPHT1;4	As(V)	110*	TLMLMVICLASGLS	110*	YGMTLMLMVICLASGLSFGS
		111	LMLMVICLASGLSF	130	SSAKGVMATLCFRFRWLGFGI
				489	VRNSLFFLAGCNVIGFFTFEL
OsPHT1;8	As(V)	115*	TLLMMVICIASGLS	45	GFFTDAYDLFCISLVTKLLGR
				115*	YGMTLMMVICIASGLSFSH
AtNIP1;1	As(III)	n.d.		161	RLLFGLDHDVCSGKHDVFIGS
AtNIP1;2	As(III)	n.d.		69	LGTYFLIFAGCAAVAVNTQHD
AtNIP3;1	As(III)	291*	EASQDEICVLRVVDVDP	274	KSYSEIRPNCKNVSSRDRQE
				291*	DRQEASQDEICVLRVVDVANQ
				306	VDPANQNYFICSSPTDINGKC
				316	CSSPTDINGKCNVTCKLAXXX
AtNIP7;1	As(III)	n.d.		35	DHPSRQRLFGLPYDIDLNPL
				183	IVVFLASALHCGPHQNLGNLT
				262	YRSISLKRTRPCSPVSPSVSS
OsNIP1;1	As(III)	n.d.		65	FGTYFLIFAGCGAVTINQSKN
OsNIP2;2	As(III)	207	LAVGSAVCITSIFAG	69	VATFLLVFVTCGAASIYGEDM
				142	YWAAQFTGAMCAAFVLRVAVLY
OsNIP3;1	As(III)	54*	KSMRCKCLPAVAEVAE	54*	YERKSMRCKCLPAVAEVAEVAE
				70	AEAWAPSAHGCVCVEIPADVVS
				173	YVAVQVLGSCAGFALKGVFH
OsNIP3;2	As(III)	n.d.		n.d.	

(continued on next page)

Table 1 (continued)

Transporter	Metalloid transported	GPS-SNO 1.0		iSNO-PseAAC	
		Cys position of S-nitrosation	Amino acid sequence	Cys position of S-nitrosation	Amino acid sequence
OsNIP3;3	As(III)	n.d.		n.d.	
OsPIP2;4	As(III)	135	LLYMAAQCLGAICGV	n.d.	
OsPIP2;6	As(III)	128	VMIYVAQCLGGIVGV	70	GYKVQSSADQCGGVGTGLIAW
OsPIP2;7	As(III)	135*	VLYVVAQCLGAIAGA	77	YKNQRATVDACTGVGYLGVAV
				99	FGATIFVLVYCTGGVSGGHIN
				135*	VRTVLYVVAQCLGAIAGAGIV
LjNIP5;1	As(III)	n.d.		168	AAQVSASICACFALKYVYHPF
LjNIP6;1	As(III)	n.d.		52	GKKKSLKNCNCFTVEEWTI
				118	KTQGAETLIGCAASTGLAVMV
				173	YIIAQMAGICASFGLKGVFN

effect at elevated concentrations due to molecular mechanisms such as protein selenization, oxidation, nitration (Kolbert et al., 2019b), and disturbance of the balance of hormones and nutrients (Kolbert et al., 2016). In the case of Se, B, and non-essential metalloids, such as As, Sb, Te, and Ge, phytotoxicity can be linked to the imbalance of reactive oxygen species (ROS) and the consequent oxidative stress. Contrarily, Si's stress-alleviating effects are realized mainly by reducing the ROS levels and the associated damages.

Beyond ROS, metalloids also modify the metabolism of reactive nitrogen species (RNS). Peroxynitrite (ONOO⁻) and S-nitrosoglutathione (GSNO), both derived from the gaseous signal molecule nitric oxide (NO), can be considered as relevant RNS (Valderrama et al., 2007). In higher plants, NO can be synthesized by oxidative and reductive reactions that involve enzymes or occur spontaneously (Kolbert et al., 2019c). NO reacts with thiol (SH)-containing proteins and peptides, forming low-molecular-weight S-nitrosothiols (SNOs), such as GSNO (Hogg, 2000; Foster et al., 2003), which is the most abundant SNO that can liberate NO or be reduced by GSNO reductase (GSNOR) (Barroso et al., 2006; Corpas et al., 2008; Leterrier et al., 2011).

The perception and transduction of the NO signal are believed to be realized primarily through the tyrosine nitration, metal nitrosylation, and S-nitrosation of proteins (Umbreen et al., 2018). NO can indirectly influence protein activity through the formation of ONOO⁻, leading to protein tyrosine nitration, which is an irreversible modification due to the formation of 3-nitrotyrosine-containing nitro-proteins (Souza et al., 2008). In plant cells, protein tyrosine nitration mainly inhibits enzyme activity (Kolbert et al., 2017) and may prevent or induce tyrosine phosphorylation, ultimately influencing cell signaling (Souza et al., 2008). S-nitrosation is a reversible reaction affecting Cys thiol groups, leading to the formation of S-nitroso-proteins with altered activity, subcellular localization, and interactions or binding activities (Lubega et al., 2021). There are many types of antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), peroxiredoxins, and the enzymes of the ascorbate–glutathione cycle, the activity of which is positively or negatively regulated by NO-dependent S-nitrosation or tyrosine nitration, or both (Begara-Morales et al., 2016). In addition, it has been widely accepted that NO is involved in plant responses to heavy metals partly via the regulation of antioxidant activities (Terrón-Camero et al., 2019). In recent years, there is an increasing evidence that NO also participates in metalloid stress regulation.

This review collates, discusses, and evaluates the accumulated literature with regard to the metabolic, signaling, and physiological role of NO and its derivatives in the plants exposed to metalloids to suggest the research directions for future studies. Additionally, using *in silico* prediction tools, we examined the possible involvement of the NO-dependent S-nitrosation of proteins in plant metalloid uptake.

2. Metalloid uptake by plants and its putative regulation by NO

The hydrophilic nature of metalloids in aqueous solutions necessitates the help of transmembrane proteins driven by concentration gradients or pumps in facilitation of metalloid movement across the plasma

membrane.

In case of limited B supply, aquaporins and aquaglyceroporins such as ZmPIP1, AtNIP5;1, AtNIP6;1, HvPIP1;3, and HvPIP1;4 have been demonstrated to facilitate B transport (Fitzpatrick and Reid, 2009; Dordas et al., 2000; Dordas and Brown, 2001a; Takano et al., 2002, 2006, 2008). However, no specific solute pumps have been identified for the active transport of B. In the presence of sufficient B, the passive diffusion of uncharged, small boric acid (H₃BO₃) without solute channel facilitators satisfies the demand of plants for B (Dordas and Brown, 2001b; Zangi and Filella, 2012). Conversely, efflux is an active transport catalyzed by BOR1 and BOR2 transporters in *Arabidopsis* (Yoshinari and Takano, 2017). BOR transporters regulate B uptake under B-deficient conditions (Tanaka et al., 2008), whereas they are degraded in case of excess B (Aibara et al., 2018; Hrmova et al., 2020).

Similar to B, Si uptake is possible in the form of uncharged Si(OH)₄ (Aho and Brzezinski, 1999). In rice, the low silicon rice 1 (*OsLsi1*) gene encodes a plasma membrane protein belonging to the Nodulin26-like intrinsic protein (NIP) subfamily of aquaporins (Ma et al., 2006). The expression level of *OsLsi1* is regulated by Si supplementation. *OsLsi1* homologs in barley (*HvLsi1*, Chiba et al., 2009) and maize (*ZmLsi1*, *ZmLsi6* (Mitani et al., 2009)) have also been characterized. Silicon efflux is catalyzed by the plasma membrane protein encoded by the low silicon rice 2 (*OsLsi2*) gene. Additionally, active Si uptake in the form of anions has been observed in marine diatoms. Sodium-requiring channels are involved in this process (Hildebrand et al., 1998; Mandlik et al., 2020).

The uptake of Se in the form of Se(VI) is based on its similarity to sulfate and mediated through the activity of sulfate transporters (Trippe and Pilon-Smits, 2021). In *Arabidopsis thaliana*, *SULTR1;2* and *SULTR1* were found to be responsible for the internalization of selenate into the plant cell (El Kassis et al., 2007). However, it seems that *SULTR1;2* is the predominant transporter for absorbing selenate via the root system (Shibagaki et al., 2002; El Kassis et al., 2007). According to Li et al. (2008), the Se(IV) uptake in wheat, mediated by active transport, is significantly inhibited by the metabolic inhibitor carbonyl cyanide m-chlorophenyl hydrazone. Further analysis reveals that the phosphate transport system may be involved in the Se(IV) uptake (Zhang et al., 2014). Additionally, the Silicon Influx Transporter *OsNIP2;1* has been demonstrated to mediate Se(IV) uptake in rice (Zhao et al., 2010).

Owing to its similarity to phosphate (Pi), As(V) is taken up by plant cells via the Pi transport systems; several phosphate transporters have been identified for the As(V) uptake and translocation in various plant species, such as AtPHT1;1, AtPHT1;4, AtPHT1;7, AtPHT1;8, and AtPHT1;9 in *Arabidopsis* and OsPHT1;1, OsPHT1;4, and OsPHT1;8 in rice. Similarly, several aquaporins involved in As(III) transport have been identified. AtNIP1;1, AtNIP1;2, AtNIP3;1, AtNIP5;1, AtNIP6;1, and AtNIP7;1 in *Arabidopsis*; OsNIP1;1, OsNIP2;1 (*OsLsi1*), OsNIP2;2 (*OsLsi6*), OsNIP3;1, OsNIP3;2, OsNIP3;3, OsPIP2;4, OsPIP2;6, and OsPIP2;7 in rice; HvNIP1;2 in barley; and LjNIP5;1 and LjNIP6;1 in *Lotus japonicus* have been demonstrated to assist in the passive transport of As(III) (Garbinski et al., 2019; Tang and Zhao, 2020).

Contrary to the As(V) uptake, the mechanism of the Sb(V) uptake has not been identified, but it may not involve phosphate transporters

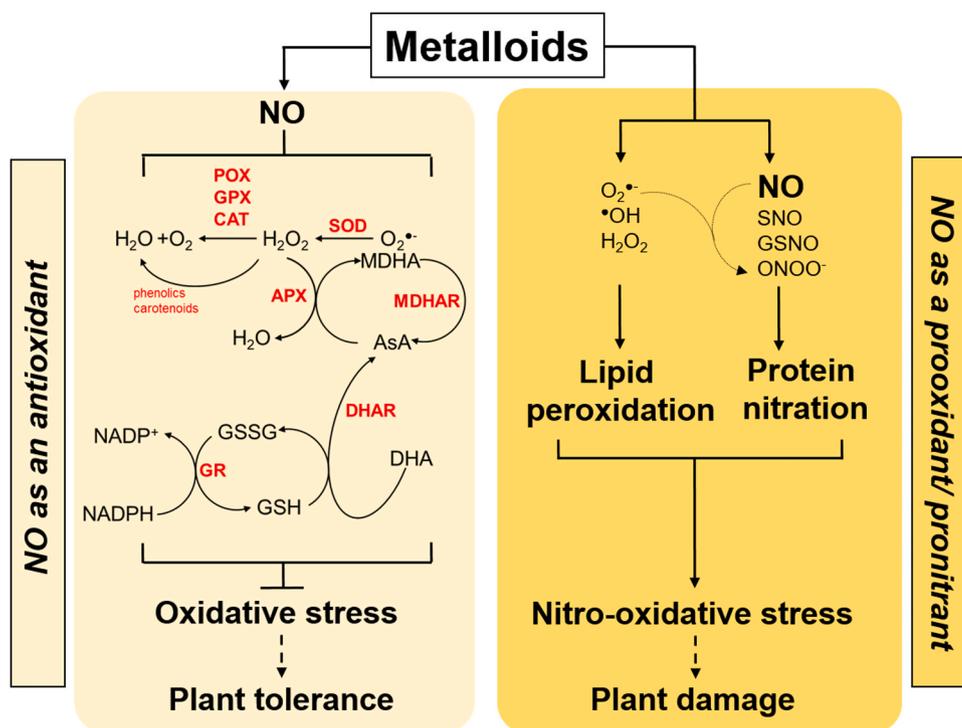


Fig. 1. The antioxidant and prooxidant/pronitrant roles of NO/RNS in metalloid-induced stress mitigation and damages in plants. Metalloid-induced NO upregulates antioxidant enzymes and non-enzymatic antioxidants, reducing oxidative stress and improving tolerance. The nitric oxide-regulated elements of the antioxidant system are indicated in red. Depending on their hazardous nature and concentration, metalloids induce accumulation of ROS and RNS, causing nitro-oxidative stress, as indicated by lipid peroxidation, protein nitration, and plant damage. Abbreviations: NO, nitric oxide; $O_2^{\cdot-}$, superoxide anion; H_2O_2 , hydrogen peroxide; MDHA, monodehydroascorbate; MDHAR, monodehydroascorbate reductase; AsA, ascorbic acid; APX, ascorbate peroxidase; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; GSSG, oxidized glutathione; GSH, reduced glutathione; GR, glutathione reductase; OH⁻, hydroxyl radical; SNO, S-nitrosothiol; GSNO, S-nitrosoglutathione; ONOO⁻, peroxynitrite.

(Zangi and Filella, 2012). However, NIPs are involved not only in the As (III) uptake but also in the entry of Sb(III) into the cells (Pommerrenig et al., 2015; Zhu et al., 2020).

Since metalloid transporters are proteins and NO signaling is achieved mainly by posttranslational modifications, NO may regulate proteins via S-nitrosation, increasing or decreasing their metalloid transport activity. This hypothesis was tested *in silico*. The S-nitrosation of the most relevant metalloid transporters was predicted using two independent software tools (peptide sequences were extracted from UNIPROT (www.uniprot.org) and submitted to the prediction software GPS-SNO 1.0 (<http://sno.biocuckoo.org>, Xue et al., 2010) and iSNO-PseAAC (<http://app.aporc.org>, Xu et al., 2013). For most metalloid transporters, the S-nitrosation of one or more Cys in them was predicted by both tools (Table 1), supporting the theoretical possibility of protein-level regulation of metalloid transport by NO. However, it should be noted that the S-nitrosation of metalloid transporter proteins may also affect the uptake of essential elements, such as phosphate and sulfate, as well as the transport of water in plant cells.

3. The involvement of NO in regulating metalloid stress responses

3.1. Nitric oxide regulates plant responses to B deficiency and toxicity

Boron is a unique micronutrient for plants owing to its narrow range of beneficial and toxic concentrations. Most of the available literature focuses on excess B-induced phytotoxicity, and only a few studies involving NO examine plants' physiological and molecular responses to B deficiency.

According to Kobayashi et al. (2018), B deficiency results in rapid cell death within the root apex of *Arabidopsis*. Using pharmacological treatments, ROS have been shown to participate in the induction of cell death in response to B deprivation. The production of ROS is thought to be triggered by stretching of the plasma membrane and the influx of calcium (Ca) ions via the mechanosensitive channels. Furthermore, NO formation is increased in B-deficient roots. Decreasing the level of NO with 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide

(cPTIO), or with the inhibitor of mammalian nitric oxide synthase (NOS), N^G-monomethyl-L-arginine (L-NMMA), mitigates cell death. These findings suggest that in addition to ROS, NO is required for B deficiency-induced programmed cell death. Another interesting result obtained from this study is that B limitation triggers transcriptome changes resembling pathogen-induced responses, suggesting that B deficiency induces ROS- and NO-associated hypersensitive response in *Arabidopsis* roots as a response to damages in the cell wall structures.

Recently, Kaya et al. (2019) observed that, similar to B deficiency, B toxicity promoted endogenous NO production in the leaves of two wheat cultivars. This finding was explained by the activation of a NOS-like enzyme by excess B. However, because no NOS enzyme has been identified in higher plants, these results should be treated with caution. The B toxicity-reducing effect of thiourea (TU) treatment, achieved by, among other things, the reduction of hydrogen peroxide (H_2O_2), electrolyte leakage, and lipid peroxidation (LPO), has also been presented. Contrarily, TU treatment further increases NO levels and NOS-like activity in the leaves of wheat cultivars. By examining several growth, oxidative, and antioxidant parameters, TU-induced tolerance against B toxicity was found to be eliminated by cPTIO-triggered NO depletion. These data confirm that NO is an essential component in the regulation of plant tolerance to excess B. The same research group revealed that thiamine-induced NO was essential in the amelioration of B toxicity in pepper plants (Kaya et al., 2020a).

The possibility that NO mitigates B toxicity was studied for the first time by Aftab et al. (2012), who observed that the addition of B or aluminum to soil significantly reduced the yield and growth of *Artemisia annua* and decreased the photosynthetic rate, stomatal conductance, intracellular CO_2 concentration, and total chlorophyll content. The application of the NO donor, sodium nitroprusside (SNP), improved the growth and photosynthetic performance of stressed and non-stressed plants. The artemisinin content was also increased in B-exposed *Artemisia annua* plants by the addition of NO. In the study by Kaya and Ashraf (2015), elevated B levels caused a significant decrease in dry biomass and fruit yield of tomato plants compared with the non-stressed plants. Excess B increased electrolyte leakage and LPO and promoted ROS production as well as antioxidant protection. The foliar application

of SNP improved biomass production and fruit yield and decreased B-induced oxidative damages and antioxidant enzyme activities. The macroelement homeostasis in tomato leaves was improved. At the same time, the B concentration in the tissues was reduced by SNP treatment (Kaya and Ashraf, 2015). This indicates that NO downregulated the uptake of B. In another study, watermelon plants were exposed to 0 (deficiency), 0.5 (standard supplementation), and 10 mg/L (excess) B concentrations with or without SNP (Farag et al., 2017). B toxicity-triggered growth inhibition of the seedlings was associated with high B translocation to the shoot tissues, causing LPO and chlorophyll depletion. Contrarily, B deficiency accelerated ROS production, mainly hydroxyl radical ($\cdot\text{OH}$), and induced oxidative injury. SNP enhanced chlorophyll content and photosynthesis, consequently inducing biomass production in B-deficient and B-excess watermelon seedlings through the reduction of B accumulation, LPO, and ROS generation. SNP also activated antioxidant enzymes, such as SOD, peroxidase (POD), and ascorbate peroxidase (APX), thus protecting the seedlings from ROS-induced oxidative damage.

The results discussed above indicate that both B deficiency and toxicity upregulate NO formation, causing its overproduction. Although NOS-like activity is assumed to be responsible for NO synthesis in both cases, the existence of a NOS in higher plants is uncertain. Therefore, the possibility that NO is synthesized via B supply-induced nitrate reduction should be closely examined (Eraslan et al., 2007). With regard to the role of NO, available data suggest that, depending on the amount of B, elevated NO production may contribute to the damage or increase tolerance (Fig. 1). In addition, a few studies suggest that exogenous NO mitigates the detrimental effects of B toxicity, improving the growth and yield partly by reducing B uptake. However, the molecular mechanism of NO's action on B transport remains unknown. NO administration may prevent B-induced ROS overproduction by activating antioxidant protection.

3.2. Dual participation of NO in Si-induced stress alleviation

The stress-relieving effects of Si in plants have been extensively studied, and recent studies have demonstrated NO as a regulator of Si's beneficial effects.

Pandey et al. (2016) examined the stress-mitigating effect of Si in hydroponically grown *Brassica juncea* treated with As. Si was found to improve root growth, increased the concentration of several micro- and macronutrients, decreased the total ROS and superoxide anion radical ($\text{O}_2^{\cdot-}$) levels, and enhanced the activity of antioxidant enzymes in the presence of As. As exposure increased the NO level in the root, the extent of which was moderated by Si. The authors concluded that the As-triggered accumulation of ROS and NO was reduced by Si, thereby protecting the tissues from oxidative damage. Similar effects have been observed in the treatment of young maize plants exposed to aluminum (Al) with 20-nm, spherical Si nanoparticles (NPs) (de Sousa et al., 2019). At higher Al concentrations, Si increased root and shoot biomass and improved photosynthetic parameters and pigment contents compared with the plants treated only with Al. Al mainly increased LPO, protein oxidation, and NO levels in the root, but supplementation with Si NP decreased these enhancements and promoted viability. In this comprehensive work, the activity of numerous antioxidant enzymes and the content of non-enzymatic antioxidants, such as flavonoids, polyphenols, and tocopherols, were analyzed. In most cases, the upregulating effect of Si was observed.

Also, Si was found to mitigate the stressor-induced accumulation of NO free radicals, which presumably enhanced stress tolerance. The protective effect of Si against salinity has also been demonstrated (Chung et al., 2020). Si application improved photosynthetic responses, such as transpiration rate and net photosynthesis rate in salinity-exposed soybean, along with reduced CAT, APX activities, and glutathione (GSH) content. Contrary to the previous works, this study analyzed the SNO content increased by Si as well as by salt stress. When Si was applied in

salt-treated plants, the SNO content significantly decreased. Moreover, salt stress upregulated the soybean GSNOR genes *GmGSNOR1*, *GmGSNOR2*, and *GmGSNOR3*. The effect of Si on the expression of the GSNOR genes was time-dependent, with a noticeable induction within a shorter period of 3–6 h, whereas Si reduced the expression of these genes after 12 h. Thus, it could be concluded that Si reduced oxidative and nitrosative damage by reducing the SNO levels through the upregulation of metabolizing GSNOR genes, thus increasing salt tolerance. In drought-stressed lentil plants, Si treatment was found to maintain nitro-oxidative homeostasis by balancing reactive oxygen species ($\text{O}_2^{\cdot-}$, H_2O_2) and reactive nitrogen species (NO) levels thus contributing to better tolerance (Sajitha et al., 2021).

The beneficial effects of Si in relation to NO have been studied not only in plants exposed to abiotic stresses but also in the case of biotic stressors, such as the infestation of *Orobanche ramosa*, a holoparasitic root weed in tomato (Madany et al., 2020). In this work, seed priming was performed using 20-nm, spherical Si NPs. The stress-mitigating effect of Si NPs was demonstrated by the reduction in infection, the increment in biomass production, and the improvement of photosynthetic parameters. Furthermore, Si NPs reduced LPO, H_2O_2 , and NO levels triggered by *Orobanche* infection in the root and shoot. In addition, the activity and amount of several ROS scavenging enzymes and non-enzymatic antioxidants were measured, and Si NP-induced increment was observed in almost all cases. Thus, the antioxidant defense was enhanced in the infected plants. Collectively, these works identify NO/SNO as damaging signal molecules induced by the stressors, including As, Al, salt, Cu and *Orobanche*, and Si or Si NP treatment alleviates stress by moderating NO/SNO overproduction.

In some other works, the opposite has been found. For instance, Tripathi et al. (2017) compared the effect of bulk Si on wheat subjected to UV-B stress with that of 20- to 95-nm, spherical Si NPs. The beneficial effect of Si NP manifested itself in the reduction of UVB-induced ROS production and the regulation of enzymes, including SOD, CAT, GPX, and APX, as well as non-enzymatic antioxidants, including proline (Pro), AsA, phenolics, and flavonoids. Contrarily, the level of UV-B-induced NO was enhanced by Si and Si NP. Therefore, the authors hypothesized that Si and Si NP regulate antioxidant defense through the upregulation of NO. However, direct evidence regarding the involvement of NO was not provided in this work. These observations were supported by the work of Kaya et al. (2020b), where the addition of Si was found to enhance pepper's cadmium (Cd) tolerance by lowering the leaf's Cd concentration and oxidative stress levels and promoting the antioxidant defense system, the leaf's Si content, photosynthetic traits, and plant growth as well as the NO, Pro, and hydrogen sulfide (H_2S) content. The diminution of Si-induced NO production by cPTIO reduced the activity and number of antioxidants, such as SOD, CAT, POD, AsA, and GSH, and aggravated biomass and chlorophyll loss. These results provided direct evidence of the role of Si-induced NO in the upregulation of antioxidants and alleviation of Cd-triggered oxidative stress. Moreover, copper (Cu) exposure induced NO production in *Salvia officinalis* which was further increased by Si addition. Authors concluded that Si may improve Cu tolerance via inducing NO generation which triggers defense mechanisms in *Salvia* plants (Pirooz et al., 2021).

Researchers also examined the oxidative stress-mitigating effect of Si in *Brassica juncea* exposed to silver nanoparticles (AgNPs). Although Si's beneficial effect could not be demonstrated (Vishwakarma et al., 2020), Si further increased the NO level in the AgNP-treated plants. However, the co-administration of Si and plant growth promoting rhizobacteria (PGPR) significantly improved the plant's AgNP tolerance by reducing NO and ROS accumulation and activating the AsA–GSH cycle, which presumably positively affected photosynthesis and plant fitness. These data suggest that high NO levels are associated with toxicity and that decreased NO content is associated with AgNP tolerance. Conversely, in Liang et al. (2015), the effect of Si on cell death in tobacco BY-2 cells was examined. Si treatment in the presence of ethylene synthesis inhibitor silver nitrate increased the production of NO and H_2O_2 , together

contributing to cell death.

The stress-mitigating activities of both Si and exogenous NO donor, mainly SNP, are well known. Liu et al. (2020) explored the effect of the combined treatment of Si and SNP on the growth and Cd uptake of maize. Both Si and SNP improved the photosynthesis, pigment content, biomass production, and yield parameters of the plants exposed to Cd at 35 mg/kg CdCl₂. The treatments decreased the Cd content in the vegetative organs and the grains. Meanwhile, the combined treatment elicited the most significant effects, indicating that the stress-alleviating effects of Si and SNP were additive. These results indicate that it may be possible to develop and apply a combined treatment method in maize cultivation in the future. Similarly, the combined application of Si and NO ameliorated the Cd-triggered oxidative damage by upregulating the AsA-GSH cycle in wheat seedlings (Singh et al., 2020a). Moreover, the As(III) uptake and oxidative stress were mitigated by the combined application of Si and SNP to *Brassica juncea* plants (Ahmad et al., 2021). These results indicate the synergistic effect of Si and NO on stressed plants.

Most of the experiments discussed above also examined the effect of Si on healthy plants, but their results are quite diverse. The growth-stimulating effect of Si accompanied by increased tissue NO levels has been described in Indian mustard, wheat, and tomato grown under stress-free conditions (Vishwakarma et al., 2020; Tripathi et al., 2017; Madany et al., 2020). Si treatment was found to upregulate the synthesis of polyamines (Manivannan and Ahn, 2017), which theoretically may be a substrate for oxidative NO synthesis (Tun et al., 2006). Si-induced nitrate reductase (NR) (Gottardi et al., 2012) may also contribute to the elevated NO levels, but the mechanism by which Si increases the NO level requires further investigation. However, in other experiments, Si alone did not affect the growth or NO content of the non-stressed plants (Pandey et al., 2016; Kaya et al., 2020b). This suggests that the growth-inducing activity of Si in healthy plants may be related to the changes in the tissue NO content. This assumption is supported by the critical role of NO in growth regulation (Sanz et al., 2015); future experiments should focus on elucidating this issue. Depending on the type of the stress, abiotic such as Al, As, salt, Cu, Cd, and UV-B, or biotic such as *Orobanche* infection, Si modulates endogenous NO levels differently. In some experimental systems, NO acts as a stress/ROS scavenger and contributes to stress-induced damages in other systems (Fig. 1). Under stress conditions, NO may play protective or damaging roles depending on its local concentration (Fancy et al., 2017); this may also be the case with Si-induced stress mitigation.

3.3. Nitric oxide contributes to the beneficial effects and phytotoxicity of Se, and NO also regulates Se uptake and metabolism

The range is narrow between the beneficial and toxic concentrations of Se, similarly to other metalloids. Only a few studies have investigated the involvement of NO in plant responses to beneficial Se concentrations. For instance, Hajiboland et al. (2019) studied the well-known Se-delayed senescence (Xue et al., 2001; Djanaguiraman et al., 2004, 2005; Kolbert et al., 2019a) in *Brassica napus*. The foliar application of Se increased NO production in young and old leaves, and a correlation was observed between the NO levels and the improvement in the photosynthetic parameters in senescent leaves. These results indicate that Se delays leaf senescence in a ROS-independent but NO-related manner, upregulating the genes involved in photosynthesis while downregulating the senescence-associated genes. The foliar application of low Se doses at 6, 8, and 10 mg/L increased the stem length and leaf number of *Stevia rebaudiana* plants without significantly inhibiting photosynthesis. The beneficial effects of Se were accompanied by the Se concentration-dependent regulation of GSNOR protein levels and protein tyrosine nitration, indicating that the beneficial doses of Se induces nitrosative signaling in *Stevia* leaves (Borbély et al., 2021). The indirect evidence for the involvement of NO in the beneficial effects of Se should be supported by further research as the low-dose Se may be used in crop

production and biofortification practices. According to the recent results of the study by Abedi et al. (2021), the low concentration of nano Se at 4 mg/L exerted beneficial effects on the growth of chicory seedlings; the effect was further enhanced by the addition of NO (SNP). Moreover, secondary metabolism was synergistically enhanced by nano Se and NO. However, the higher dose of nano Se at 40 mg/L triggered negative effects on biomass and flowering; the adverse effects were ameliorated by the addition of NO (Abedi et al., 2021).

It has been demonstrated that Se exposure causes a disturbance in RNS metabolism. In the early stage of seedling development, NO levels are decreased by Se but increase in the longer term (Lehotai et al., 2012). In another experiment, Se-induced cytokinins (CK) were observed to reduce the NO content in *Arabidopsis* roots (Lehotai et al., 2016a). Recently, it was found that in the Se-stressed roots, the ethylene (ET) levels were increased, whereas NO generation was reduced. Since NO negatively influences the ET levels, Se exposure creates a feedback loop, resulting in lateral root outgrowth (Feigl et al., 2019).

Se toxicity also depends on the plant species, which can be categorized as non-accumulators, accumulators, and hyperaccumulators. Most research involving NO analyzes the effect of toxic Se concentrations on plant species with varying levels of tolerance. The NO/GSNO-overproducing *Arabidopsis* mutant, *gsnor1-3*, was more resistant, but the NO-deficient *nia1nia2* mutant exhibited a more pronounced sensitivity to Se stress than the wild type. These data suggest that endogenous NO may contribute to Se tolerance (Lehotai et al., 2012). However, Chen et al. (2014) associated Se-induced NO production with ROS formation and Se toxicity in *Brassica rapa* roots. These results were supported by Lehotai et al. (2016b), who demonstrated that Se treatment promoted the production of NO and ONOO[•] in pea organs and caused toxicity due to protein tyrosine nitration. In addition, selenite caused more severe protein nitration and toxicity than selenate in *Brassica juncea* (Molnár et al., 2018a). However, the Se-sensitive *Arabidopsis thaliana* suffered more severe oxidative stress but milder nitrosative stress compared with the Se-tolerant *B. juncea* (Molnár et al., 2018b). This suggests that selenite tolerance and sensitivity were more tightly associated with oxidative processes in these species. In a comparative study, Se seriously affected the metabolism of RNS via NO production, the ONOO[•] and GSNO levels, and the GSNOR activity and protein nitration in Se-sensitive *Astragalus membranaceus*, whereas no relevant Se-induced changes were observed in Se-hyperaccumulator *Astragalus bisulcatus*, indicating a correlation between RNS-induced nitrosative stress and Se tolerance (Kolbert et al., 2018, 2019b).

There is also evidence of the influence of exogenous NO (SNP) on the Se uptake and speciation in rice. According to Xiao et al. (2017), SNP stimulates GSH biosynthesis and triggers Se metabolism in rice seedlings exposed to a moderate Se concentration at 6 μM. In addition, SNP supplementation induced the expression of phosphate and sulfate transporter genes encoding OsPT2, OsSultr1;2, and OsSultr4;1, increasing the selenocysteine (SeCys) and selenomethionine (SeMet) contents in rice roots. Conversely, Dai et al. (2020) reported that SNP promoted growth and photosynthesis; enhanced antioxidant capacity; downregulated the expressions of OsPT2, OsSAMS1, and OsSBP1 genes in the roots and OsPT2, OsCS, and OsSBP1 genes in the shoots; and reduced the Se uptake in rice seedlings subjected to severe Se treatment at 25 μM. The seemingly contradictory results highlight the possibility of SNP exerting opposite effects on the Se uptake and metabolism depending on the magnitude of the Se exposure. Furthermore, NO seems to exert its regulatory role on the Se uptake at the gene expression level.

Collectively, beyond ROS imbalance and protein oxidation, toxic Se concentrations disrupt endogenous RNS metabolism in non-hyperaccumulator plant species, such as *Arabidopsis thaliana*, *Brassica rapa*, *Brassica juncea*, *Pisum sativum*, and *Astragalus membranaceus*, and increase protein tyrosine nitration, contributing to secondary nitro-oxidative stress and ultimately to Se phytotoxicity (Kolbert et al., 2019b). Furthermore, data suggest that Se-mediated NO antagonizes phytohormones, such as CK and ET, and their interplay regulates root

development during Se stress. Not only does Se affect endogenous NO/RNS metabolism, but NO content increased by SNP also positively or negatively regulates the Se uptake and speciation within the plant tissues depending on the Se concentration.

3.4. Arsenic modulates NO/RNS metabolism and exogenous NO mitigates As toxicity via numerous pathways

Arsenic causes damage to all organisms, including plants; however, the rate of its toxicity depends on the form of As and the plant species. While most of the published experiments focus on the beneficial effect of exogenous NO donors on As-induced damages, other works analyze the As-induced changes in endogenous NO/RNS metabolism (Sharma et al., 2021).

The observed effects of As on endogenous NO and RNS levels are variable. As(III) exposure was found to increase NO levels in the rice root (Rao et al., 2011). Moreover, As(V) exposure in *Arabidopsis* (Letierrier et al., 2012), rice (Kushwaha et al., 2019; Solórzano et al., 2020), *Vicia faba* guard cells (Xue and Yi, 2017), and *Spirodela intermedia* (Da Silva et al., 2018) was demonstrated to increase NO levels. Contrarily, decreased NO levels were measured in As(V)-treated pea (Singh et al., 2015; Rodríguez-Ruiz et al., 2019) and maize seedlings (Kaya et al., 2020c) compared with the untreated plants. According to Letierrier et al. (2012), As(V) increased GSNOR activity, decreased GSNO levels and $O_2^{\cdot-}$ production, and increased protein nitration, supporting As-triggered nitro-oxidative stress in *Arabidopsis* (Fig. 1). Recently, Rodríguez-Ruiz et al. (2019) observed that protein oxidation and LPO increased in As(V)-treated pea. Still, the nitrosative parameters such as ONOO⁻, NO levels, and GSNOR activity demonstrated As-induced diminution in this experimental system. Therefore, As likely regulates ROS and RNS signaling differently.

Further studies examine the stress-mitigating or damage-inducing effect of endogenous NO on plants. NO participates in the induction of As-triggered cell death, as was shown in the *Vicia faba* guard cells by Xue and Yi (2017). As treatments caused cell death in a concentration-dependent manner and concomitantly increased the levels of NO, ROS, and Ca as well as NR activity. Arsenic-induced cell death was blocked by cPTIO, NR inhibitor sodium azide, AsA, CAT, EGTA, and Ca channel blocker lanthanum chloride, demonstrating that NO, ROS, and Ca as signal components are required for the induction of As-induced cell death in guard cells. Moreover, this work demonstrated that As caused NO formation in guard cells through NR activation (Xue and Yi, 2017).

Many other studies have proven the stress-mitigating effect of endogenous NO production on plant cells. For instance, Singh et al. (2015) found that supplementing As-exposed pea plants with H₂S promoted As tolerance by improving photosynthesis and decreasing ROS accumulation due to the upregulation of the AsA–GSH cycle. These effects were associated with the increased NO level; therefore, the authors hypothesized that H₂S contributes to As tolerance by the NO-dependent upregulation of the antioxidant defense. Furthermore, the As tolerance of mustard seedlings could be enhanced by Ca treatment and aggravated by Ca chelation (Singh et al., 2020b). Using NO scavenger cPTIO with Ca, Ca's beneficial effect on biomass production, photosynthesis, and ROS diminution was remarkably reduced in the seedlings exposed to As. This result indicates that NO is an antioxidant molecule in the Ca-induced As tolerance. Similarly, Kaya et al. (2020c) revealed that NO was a regulatory intermediate in the salicylic acid (SA)-induced As tolerance of maize. The upregulating effect of SA on the AsA–GSH and glyoxalase systems was abolished by NO scavenging. This observation can be considered as an additional evidence of the antioxidant role of NO in As tolerance. Moreover, the As(V) treatment of rice seedlings promoted the formation of new adventitious roots (AR) but reduced the length and weight of the primary root (Kushwaha et al., 2019). L-NMMA could reverse the effect of As on AR, and the levels of $O_2^{\cdot-}$ and H₂O₂ were higher in the roots treated with As and L-NMMA than in the control. The

effect of exogenous NO in this system was also examined. SNP was found to further increase the number of AR, decrease the level of ROS, and upregulate the dehydroascorbate reductase (DHAR) activity and AsA–GSH cycle in As-exposed plants. The inhibition of NOS-like activity-derived NO negatively influenced the cell-cycle dynamics, whereas SNP maintained it. Therefore, it can be concluded that NO is an endogenous regulator of As-induced AR formation that contributes to stress tolerance due to a more advanced root system.

In addition, the alleviation of As toxicity by exogenous NO donor (mostly SNP) treatments in various monocots and dicots has been uncovered (Bhat et al., 2021). Some studies apply both SNP and a NO scavenger, such as cPTIO, L-NAME, and Hb, to As-stressed plants in order to investigate the involvement of the endogenous and exogenous NO in As-triggered plant responses. In tall fescue leaves and bean seedlings, As-induced oxidative stress was characterized by the accumulation of $O_2^{\cdot-}$ and H₂O₂, the inactivation of antioxidant enzymes, and the intensified membrane damage (Jin et al., 2010; Talukdar, 2013). These adverse effects were mitigated by the SNP addition, whereas the damages were aggravated by the application of a NO scavenger such as cPTIO. These results indicate that endogenous NO upregulates antioxidant defense, thus reducing As-triggered oxidative stress. Recently, Souri et al. (2020) provided additional evidence for the beneficial role of endogenous NO in As tolerance in the hyperaccumulator species *Isatis cappadocica*. In this study, the application of bovine Hb as a NO scavenger and L-NAME as an inhibitor of mammalian NOS was found to worsen As-induced oxidative damages. Recently, the ameliorating effect of both exogenous and endogenous NO on arsenate toxicity in soybean has been demonstrated using pharmacological approach (Singh et al., 2021). Decreasing NO level by the application of L-NAME led to increased arsenate toxicity supporting that endogenous NO is involved in stress mitigation. Further results indicated that H₂O₂ may act downstream of NO signaling ameliorating arsenate toxicity (Singh et al., 2021).

Numerous studies utilized the standard experimental design, in which the control and As-exposed plants were supplemented with SNP as the exogenous NO donor at a concentration of 30–250 μM, most often 100 μM, primarily via the nutrient solution. Many results demonstrate that the use of SNP reduces As-induced ROS (mainly $O_2^{\cdot-}$, H₂O₂) overproduction and mitigates oxidative damages of lipids and DNA by upregulating a wide range of antioxidant components, such as SOD, APX, CAT, GPX, glutathione reductase (GR), POD, MDHAR, DHAR, glyoxalase I and II, AsA, GSH, phenols, and carotenoids (Singh et al., 2009, 2013, 2016, 2017a; Ismail, 2012; Farnese et al., 2013; Namdjoyan and Kermanian, 2013; Hasanuzzaman and Fujita, 2013; Saeid et al., 2014; Silveira et al., 2015; Mohamed et al., 2016; Andrade et al., 2016; Karam et al., 2017; Praveen and Gupta, 2018; Praveen et al., 2019, 2020; Chandrakar and Keshavkant, 2019; Ahmad et al., 2020). The reduction of the uptake, bioaccumulation, and translocation of As was demonstrated to be additional effects of SNP (Singh et al., 2009, 2013, 2016, 2017a, 2017b; Ismail, 2012; Namdjoyan and Kermanian, 2013; Silveira et al., 2015; Andrade et al., 2016; Praveen and Gupta, 2018; Praveen et al., 2019; Chandrakar and Keshavkant, 2019; Ahmad et al., 2020). SNP-derived NO was found to downregulate the expression of As transporters OsLis1 and OsLis2 and modulate metal transporters, particularly NIP, NRAMP, ABC, and iron transporters (Singh et al., 2016, 2017a, 2017b). Moreover, applying an NO donor activated intracellular As binding due to the promotion of heavy metal conjugating GST activity/expression and to the elevation of phytochelatin content (Singh et al., 2013, 2017b; Farnese et al., 2013). NO administration also improved the mineral nutrition of As-exposed plants by increasing the expression of genes and activity of enzymes that are involved in phosphorus, potassium, and, in particular, nitrogen and ammonium uptake and metabolism, e.g., NR, nitrite reductase, glutamate dehydrogenase, and glutamine oxoglutarate aminotransferase (Mohamed et al., 2016; Praveen and Gupta, 2018; Praveen et al., 2019, 2020).

Another beneficial effect of SNP supplementation in As-treated

Table 2

The expression of NO-modified plant genes in metalloids-exposed plants. In all cases, NO treatment was applied in the form of sodium nitroprusside (SNP), and the gene expression was analyzed via RT-PCR.

Gene symbol	Function	Plant species	Treatments	Effect	References
<i>OsSultr2;1</i> and <i>OsSultr4;1</i>	sulfate transport	<i>Oryza sativa</i>	6 μ M Se(IV), 10 μ M SNP, 6 μ M Se(IV) plus 10 μ M SNP for 4 days	all treatments cause upregulation	Xiao et al. (2017)
<i>OsPT2</i>	phosphate transport	<i>Oryza sativa</i>	6 μ M Se(IV), 10 μ M SNP, 6 μ M Se(IV) plus 10 μ M SNP for 4 days	all treatments cause upregulation	Xiao et al. (2017)
<i>OsNIP2;1</i>	silicon transport	<i>Oryza sativa</i>	6 μ M Se(IV), 10 μ M SNP, 6 μ M Se(IV) plus 10 μ M SNP for 4 days	all treatments cause downregulation	Xiao et al. (2017)
<i>Osy-ECS</i>	glutathione synthesis	<i>Oryza sativa</i>	6 μ M Se(IV), 10 μ M SNP, 6 μ M Se(IV) plus 10 μ M SNP for 4 days	all treatments cause upregulation	Xiao et al. (2017)
<i>OsGS</i>	glutathione synthesis	<i>Oryza sativa</i>	6 μ M Se(IV), 10 μ M SNP, 6 μ M Se(IV) plus 10 μ M SNP for 4 days	SNP-induced upregulation in the absence and presence of Se(IV)	Xiao et al. (2017)
<i>OsLsi1</i> and <i>OsLsi2</i>	arsenite transport	<i>Oryza sativa</i>	25 μ M, 50 μ M As(V), 100 μ M SNP, 25 μ M As (V) plus 100 μ M SNP, 50 μ M As (V) plus 100 μ M SNP for 7 days	SNP decreases the As(V)-upregulated expressions	Singh et al. (2016)
<i>OsYSL2</i> , <i>OsFRDL1</i> , <i>OsIRO2</i> , <i>OsIRT1</i>	iron transport	<i>Oryza sativa</i>	25 μ M, 50 μ M As(V), 100 μ M SNP, 25 μ M As (V) plus 100 μ M SNP, 50 μ M As (V) plus 100 μ M SNP for 7 days	SNP decreases the As(V)-upregulated expressions	Singh et al. (2016)
<i>OsLsi2</i>	arsenite transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP-induced upregulation in the absence of As(III), and downregulation in the presence of As (III)	Singh et al. (2017a, 2017b)
<i>OsNRAMP5</i>	manganese transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP-induced upregulation in the absence of As(III), and downregulation in the presence of As (III)	Singh et al. (2017a, 2017b)
<i>OsIRT1</i> , <i>OsYSL2</i>	iron transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP induced-upregulation in the absence of As(III), and downregulation in the presence of As (III)	Singh et al. (2017a, 2017b)
<i>OsLSi1</i>	arsenite transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP induced-downregulation in the absence of As(III) and in the presence of As(III)	Singh et al. (2017a, 2017b)
<i>OsFRD1</i>	iron transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP induced-downregulation in the absence of As(III) and in the presence of As(III)	Singh et al. (2017a, 2017b)
<i>OsIRO2</i>	iron transport	<i>Oryza sativa</i>	25 μ M As(III), 30 μ M SNP, 25 μ M As(III) plus 30 μ M SNP for 7 days	SNP doesn't alter the expression in the absence of As(III) and it causes downregulation in the presence of As(III)	Singh et al. (2017a, 2017b)
<i>OsPIN1a</i> , <i>OsPIN1b</i> , <i>OsPIN1c</i> , <i>OsPIN1d</i> , <i>OsPIN2</i> , <i>OsPIN5a</i> , <i>OsPIN5c</i> , <i>OsPIN8</i> , <i>OsPIN9</i> , <i>OSPIN10b</i>	auxin transport	<i>Oryza sativa</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced upregulation in the absence and in the presence of As (III)	Praaven and Gupta (2018)
<i>OsAMT</i> , <i>OsNIR</i> , <i>OsNTR</i>	nitrogen uptake and metabolism	<i>Oryza sativa</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced upregulation in the absence and in the presence of As (III)	Praaven and Gupta (2018)
<i>OsPHT</i>	phosphate uptake	<i>Oryza sativa</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced downregulation in the absence of As(III) and upregulation in the presence of As (III)	Praaven and Gupta (2018)
<i>OsKTP</i>	potassium uptake	<i>Oryza sativa</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced downregulation in the absence of As(III) and upregulation in the presence of As (III)	Praaven and Gupta (2018)
<i>BjAMT1;1</i> , <i>BjAMT2</i> , <i>BjNTR1;1</i> , <i>BjNTR1;2</i> , <i>BjNTR2;1</i> , <i>BjNTR2;7</i>	nitrogen uptake	<i>Brassica juncea</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced downregulation in the presence of As(III)	Praaven and Gupta (2018)
<i>BjNTR1</i> , <i>BjNTR2</i> , <i>BjNIR</i> , <i>BjGS1;1</i> , <i>BjGS2</i> , <i>BjGDH1</i> , <i>BjGDH2</i> , <i>BjASN2</i> , <i>BjFd-GOGAT</i> , <i>BjNADH-GOG</i>	nitrogen metabolism	<i>Brassica juncea</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced downregulation in the presence of As(III)	Praaven and Gupta (2018)
<i>BjPIN1a</i> , <i>BjPIN1b</i> , <i>BjPIN2c</i> , <i>BjPIN3</i> , <i>BjPIN5</i> , <i>BjPIN6</i> ,	auxin transport	<i>Brassica juncea</i>	150 μ M As(III), 100 μ M SNP, 150 μ M As(III) plus 100 μ M SNP, for 2 days	SNP-induced upregulation in the absence and presence of As(III)	Praaven and Gupta (2018)

(continued on next page)

Table 2 (continued)

Gene symbol	Function	Plant species	Treatments	Effect	References
<i>BjPIN7b</i> , <i>BjPIN8a</i> , <i>BjPIN8b</i> <i>GmP5CS</i>	proline synthesis	<i>Glycine max</i>	50 μ M As(III), 75 μ M SNP, 50 μ M As(III) plus 75 μ M SNP for 5 days	SNP-induced upregulation in the presence of As(III)	Chandrakar and Keshavkant (2019)

plants is the improvement of water balance by the reduction of transpiration and enhancement of sugar, glycine betaine, and Pro contents (Praveen and Gupta, 2018; Ahmad et al., 2020). Also, the production and activity of the Pro synthesis enzyme, pyrroline-5-carboxylate synthase (P5CS), was found to be induced by SNP (Chandrakar and Keshavkant, 2019). NO is also involved in the restoration of the hormone system disrupted by As since the application of SNP improved the level of the hormones, such as gibberellic acid, indole-3-acetic acid, kinetin, and benzyl adenine (Mohamed et al., 2016), and reduced the level of stress hormones, such as abscisic acid and jasmonic acid (Mohamed et al., 2016; Singh et al., 2017b). The expression of the PINOID (PIN) auxin efflux carrier gene was significantly enhanced in SNP-supplemented, As-exposed rice and mustard, possibly improving polar auxin transport and root growth (Praveen and Gupta, 2018; Praveen et al., 2019). In As-exposed *Arabidopsis*, the application of SNP enhances ROS formation, which is thought to cause IAA oxidation and consequently reduce IAA levels, thus equilibrating auxin homeostasis favoring lateral root induction (Piacentini et al., 2020a, 2020b).

A large amount of data indicates the diverse effects of NO in As-exposed plants. Beyond its antioxidant effect, NO reduces As uptake and accumulation as well as improves nutritional homeostasis, water balance, and hormonal status of plant tissues, resulting in enhanced stress endurance.

3.5. RNS contribute to Sb phytotoxicity via nitro-oxidative stress

Antimony (Sb) is a metalloid rarely studied by plant biologists, even though its accumulation in soils due to anthropogenic activity is toxic to all organisms, including plants (Feng et al., 2013).

Recently, besides ROS, the metabolism of RNS was studied in Sb-exposed sunflowers and tomatoes (Ortega et al., 2017; Espinosa-Vellarino et al., 2020). In both cases, the plants were treated in hydroponics with 0, 0.5, or 1 mM of Sb for similar periods. The accumulation of Sb was observed in the organs of both species, and it was found to reduce biomass production, chlorophyll content, and photosynthesis. Nutrient contents such as magnesium and iron were similarly decreased by Sb exposure, and most of the observed antioxidants, such as SOD, APX, GR, and POD, were induced in both species. In the root of Sb-exposed sunflowers and tomatoes, the SNO, $O_2^{\cdot-}$, and H_2O_2 levels significantly increased (Ortega et al., 2017; Espinosa-Vellarino et al., 2020), and the activity of GSNOR in sunflowers was induced mainly by the higher Sb concentration, indicating that Sb caused secondary nitro-oxidative stress (Ortega et al., 2017). In the study by Espinosa-Vellarino et al. (2020), Sb-exposed roots also exhibited elevated NO and ONOO⁻ levels, further supporting the observation that Sb exposure disturbed RNS metabolism and induced nitro-oxidative stress in plants (Fig. 1). Exogenous NO may have a protective effect against Sb stress like it did to Se, but no experimental data regarding this issue is available.

4. Conclusion

In general, NO participates as a regulator in plant responses to excess metalloids and limited metalloid supply. NO plays diverse roles depending on the broad spectrum of actions of the metalloids. Moreover, it intensifies the stress-mitigating effect of Si, whereas in the case of Se, As, and Sb, the accumulation of NO/RNS contributes to toxicity. It

promotes the positive effect of low concentrations of Se and enhances the damage caused by B deficiency. The participation of endogenous NO/RNS in metalloid-induced stress mitigation or damage is presented in Fig. 1. Additionally, the exogenous application of NO donor SNP reduces B, Se, and As toxicity. The current data suggest that the *general role of NO common for all metalloids* is to relieve secondary oxidative stress due to the activation of antioxidant defense at the level of protein activity and gene expression. Moreover, NO has been demonstrated to regulate the expression of genes involved in phytohormone metabolism, transport, nutrient transport, and nitrogen metabolism in metalloid-exposed plants. In some cases, such as Se, the NO-dependent regulation of metalloid-specific uptake systems at the gene expression level has been suggested; these can be considered as *metalloid-specific NO effects*. Also, the genes involved in the plant responses to metalloids affected by exogenous NO are summarized in Table 2.

5. Future perspectives of the research field

According to the cited publications, the research field on NO in plant responses to metalloids is relatively novel. So far, the studies have mainly described the effects of NO. However, in the near future, it is important to shift the research direction toward the examination of the molecular mechanisms of NO-dependent signaling. Protein targets of metalloid-induced S-nitrosation and tyrosine nitration should be characterized to explain the effects of NO.

Based on *in silico* prediction, we propose S-nitrosation as a putative mechanism for the NO-associated regulation of metalloid transporters; such a proposal needs to be supported by future experimental data. Furthermore, it is important to examine the expression of the NO-induced genes in plants exposed to metalloids and the genes involved in NO metabolism to further elucidate their molecular mechanisms. Methodological developments, such as the application of NO donors other than SNP such as GSNO and NO-releasing nanomaterials, are also necessary. In the case of SNP application, it is recommended to verify the NO-releasing capacity and investigate the reversibility of the effects using a NO scavenger. In several studies, inhibitors of mammalian NOS were used; such an approach should be treated with caution as the homolog of the enzyme in higher plants remains unidentified. At the same time, it is important to explore the unknown pathways of NO metabolism regulated by metalloids. Given the currently increasing environmental contamination worldwide, there is great potential in applying NO to mitigate metalloid stress. However, studying the regulatory role of NO is the requisite of its application.

CRedit authorship contribution statement

Zsuzsanna Kolbert: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. **Attila Ördög:** Software, Visualization, Writing – review & editing.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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