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An update on nitric oxide and its benign role in plant responses under metal stress

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A R T I C L E I N F O

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A B S T R A C T

Pollution due to heavy metal(loid)s has become common menace across the globe. This is due to unprecedented frequent geological changes coupled with increasing anthropogenic activities, and population growth rate. Heavy metals (HMs) presence in the soil causes toxicity, and hampers plant growth and development. Plants being sessile are exposed to a variety of stress and/or a network of different kinds of stresses throughout their life cycle. To sense and transduce these stress signal, the signal reactive nitrogen species (RNS) particularly nitric oxide (NO) is an important secondary messenger next to only reactive oxygen species (ROS). Nitric oxide, a redox active molecule, colourless simple gas, and being a free radical ($NO^•$) has the potential in regulating multiple biological signaling responses in a variety of plants. Nitric oxide can counteract HMs-induced ROS, either by direct scavenging or by stimulating antioxidants defense team; therefore, it is also known as secondary antioxidant. The imbalance or cross talk of/between NO and ROS concentration along with antioxidant system leads to nitrosative and oxidative stress, or combination of both i.e., nitro-oxidative stress. Endogenous synthesis of NO also takes place in plants in the presence of heavy metals. During HM stress the different organelles of plant cells can biosynthesize NO in parallel to the ROS, such as in mitochondria, chloroplasts, peroxisomes, cytoplasm, endoplasmic reticulum and apoplasts. In view of the above, an effort has been made in the present review article to trace current knowledge and latest advances in chemical properties, biological roles, mechanism of NO action along with the physiological, biochemical, and molecular changes that occur in plants under different metal stress. A brief focus is also carried on ROS properties, roles, and their production.

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Abbreviations

•NO	Nitric oxide radical
$_1O^2$	Singlet oxygen
$^3Chl^*$	Chlorophyll triplet
$^3O_2$	Dioxygen
Acetyl-CoA	Acetyl coenzyme A
Apo	Apoplast
$_{apo}$ROS	Apoplastic reactive oxygen species
*At*NOS	*Arabidopsis thaliana* Nitric Oxide Synthase
Chl	Chlorophyll
cNR	Cytosolic nitrate reductase
CO_2	Carbon dioxide
Cyt *b*	Cytochrome *b*
Cyt *c*	Cytochrome *c*
Cyt P_{450}	Cytochrome P_{450}
Cyt	Cytoplasm
$_{cyt}$ROS	Cytoplasmic reactive oxygen species
ER	Endoplasmic reticulum
ETC	Electron transport chain
Fe-S	Iron-Sulphurcentre
FMN	Flavin mononucleotide
FNR	Ferredoxin
GPx	Glutathione-dependent peroxidase
GR	Glutathione reductase
GSH	Glutathione reduced
GSNO	S-nitrosoglutathione
H_2O_2	Hydrogen peroxide
HNO_2	Nitrous acid
HO_2	Hydroperoxy radical
HOCl	Hypochlorous acid
MDA	Malonicdialdehyde
Mit	Mitrochondria
mtETC	Mitochondrial electron transport chain
N_2O_3	Dinitrogen trioxide
N_2O_4	Dinitrogen tetroxide
Ni-NOR	Nitrite-nitric oxide reductase
NiR	Nitrite reductase
NO^-	Nitroxyl anion
NO•	Nitric oxide radical
NO^+	Nitrosylcation
NO_2•	Nitrogen dioxide
NO_2^+	Nitronium anion
NO_2Cl	Nitryl chloride
NOSLE	Nitric oxide synthase like enzyme
NR	Nitrate reductase
$O_2^{-•}$	Superoxide
O_3	Ozone
OH•	Hydroxyl radical
$ONOO^-$	Peroxynitrite
PPTMs	Protein Post-Transitional Modifications
P_{680}	Primary electron donor in PSII
P_{700}	Primary electron donor in PSI
Pero	Peroxisome
PM	Plasma membrane
PM-NR	Plasma membrane-bound nitrate reductase
Q_A	Primary quinone acceptor in PSII
RBOHs	Respiratory Burst Oxidase Homologs
RNS	Reactive Nitrogen Species
RO•	Alkoxyl radical
RO_2•	Peroxyl radical
ROONO	Alkyl peroxynitrites
ROS	Reactive oxygen species
RuBP	Ribulose-1,5-bisphosphate
SNAP	S-nitroso-N-acetylpenicillamine
SNP	Sodium nitroprusside
SOD	Superoxide dismutase
Tyr	Tyrosine
XDH	Xanthine oxidase/dehydrogenase

1. Introduction

The present era is facing an unprecedented rapid/frequent climatic change [1], which is mainly originated due to growing population coupled with diverse anthropogenic activities like combustion of fossil fuels, mining, disposal of industrial wastes, use of imbalance fertilizers and pesticides, spillage of petrochemicals, e-wastes, coal based thermal power plants, fluorescent lamps, electrical appliances, battery industry, ceramics and pollution [2]. Heavy metals are an ill-defined group of inorganic chemical hazards such as., Cr, Cd, Pb, As, Cu, Hg, Ni, Zn etc. Excess of HMs has become a dangerous problem to agriculture and environment as they enter into food chain or food web in its own ways, causing severe health concerns to human [[3] and references therein]. Once metal concentrations reach into soil at toxic level, they hamper the plant growth and development by altering their physiological and metabolical processes. Heavy metal toxicity occurs by the mechanisms under Fenton reaction or their ability to bind strongly to oxygen, nitrogen and sulphur atoms. Toxicity caused by HMs strongly ensures oxidative damages by quenching reactive free radicals or reactive oxygen species (ROS), which is constantly produced in cellular compartments (chloroplast, mitochondria, peroxisomes, cytosol and apoplastic spaces). The generated oxidative reactions disrupt the antioxidant machinery by inactivating the enzymes [4], along with various morpho-physiological and biochemical dysfunctions in plants [[2] and references therein]. Furthermore, HMs toxicity also occurred by their affinity to displace any essential cations of cells. Nitric oxide (NO), a new gaseous compound after ethylene is reported to play a key role to counteract HMs-induced ROS, either by direct scavenging ROS or by stimulating antioxidants defense team in plants. NO has also been reported to induce resistance and tolerance response in plant against HMs such as Cd, Cu, Ni, Zn, and As [5]. Recognized as chemistry rich compound and as a novel biological signaling messenger, NO is receiving special attention continuously from the areas of free radical research in the branches of biological and molecular sciences, including medicine, biochemistry, physiology, genetics, and biotechnology. Furthermore, there are increasing evidences corroborating the benign role of NO molecule in plant responses to metal stress. Therefore, in this review, an effort has been made to cover latest advances in chemical properties, biological roles, and mechanism of its biosynthesis, with special emphasis on effect of NO on physiological, biochemical and morphological changes that occur in plants under different metal treatment condition due to exogenously applied NO. A brief focus is also carried on ROS properties, roles, and their production. A hypothetical based model of a mode of NO action during cross talk with ROS under metal stress is also proposed.