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Review

Implication of nitric oxide (NO) in excess element-induced morphogenic responses of the root system

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ABSTRACT

Extremes of metal and non-metal elements in the soils create a stressful environment and plants exposed to sub-lethal abiotic stress conditions show a broad range of morphogenic responses designated as stress-induced morphogenic response (SIMR). Being the first plant organ directly contacting with elevated doses of elements, the root system shows remarkable symptoms and deserves special attention. In the signalling of root SIMR, the involvement of phytohormones (especially auxin) and reactive oxygen species (ROS) has been earlier suggested. Emerging evidence supports that nitric oxide (NO) and related molecules (reactive nitrogen species, RNS) are integral signals of root system development, and they are active components of heavy metal-induced stress responses as well. Based on these, the main scope of this review is to demonstrate the contribution of NO/RNS to the emergence of excess element-induced root morphogenic responses. The SIMR-like root system of lead-treated *Arabidopsis thaliana* contained elevated NO levels compared to the root not showing SIMR. In NO-deficient *nia1nia2* plants, the degree of selenium-induced root SIMR was, in some characteristics altered compared to the wild-type. Moreover, among the molecular elements of SIMR several potential candidates of NO-dependent S-nitrosylation or tyrosine nitration have been found using computational prediction. The demonstrated literature data together with own experimental results strongly outline that NO/RNS are regulating signals in the development of root SIMR in case of excess metal and non-metal elements. This also reveals a new role of NO in acclimation emphasizing its importance in defence mechanisms against abiotic stresses.

Contents

Abbreviations: CK, Cytokinin; cPTIO, 2-(4-carboxyphenyl)-4,5-dihydro-4,4,5,5-tetramethyl-1-imidazollyl-1-oxy-3-oxide; ET, Ethylene; H_2O_2, Hydrogen peroxide; LR, Lateral root; NO, Nitric oxide; PR, Primary root; RNS, Reactive nitrogen species; ROS, Reactive oxygen species; SIMR, Stress-induced morphogenic response; SNP, Sodium nitroprusside.

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1. Excess element-induced morphogenic responses of the root system: common features induced by different conditions

Due to their cumulative effects and long-term interactions, the inordinate accumulation of different metal (e.g. heavy metals like copper, Cu; cadmium, Cd; lead, Pb) and non-metal (e.g. selenium, Se; bromine, Br) elements in the soils can be a challenge for living organisms, especially for plants. Being sessile organisms, the reorientation of growth is the only option for plants to survive e.g. in an environment exposed to excess doses of elements. The common morphological symptoms of this developmental adaptation were determined and their manifestation was named as stress-induced morphogenic responses (SIMR, Potters et al., 2007). After a literature survey, it's evident that during excess element-triggered SIMR the main target is the root system, which is not surprising giving the fact that it is the first organ growing in the soil. Therefore this organ is in direct contact with the high doses of elements. Furthermore, in case of excessive external supply, the uptake of elements is often accompanied by their disproportionate accumulation in root cells. For the above reasons, roots show alterations in their growth and morphology as a part of their SIMR. At cellular

Table 1
Overview of root morphogenic responses induced by the excess of different elements. Only publications reporting decreased root elongation accompanied by concomitant increase in lateral/seminal root number are indicated.

Element	Concentration	Duration	Growth medium	Species	References
Essential microelements					
Cu	30–50–100 μM $CuSO_4$	7 days	agar	*Arabidopsis thaliana*	Pasternak et al., 2005
Cu	10 μM $CuSO_4$	17 days	agar	*Arabidopsis thaliana*	Kolbert et al., 2012
Cu	10 μM $CuSO_4$	7 days	solution	*Brassica juncea*, *Brassica napus*	Feigl et al., 2013
Cu	1 μM $CuSO_4$	4 weeks	solution	*Pinus pinaster*	Arduini et al., 1995
Cu	5 or 25 mg L^{-1} $CuSO_4$	14 days	solution	*Triticum aestivum*	Singh et al., 2007
Cu	50 μM $CuSO_4$	8 days	agar	*Arabidopsis thaliana*	Lequeux et al., 2010
Cu	0.66 μM, 1.17 μM Cu	4 weeks	solution	*Chloris gayana* Knuth.	Sheldon and Menzies, 2005
Cu	13 μM g^{-1} soil	2 months	soil	*Origanum vulgare*	Panou-Filotheou and Bosabalidis, 2004
Cu	10 μM $CuSO_4$	3 days	solution	*Triticum aestivum*	Mahmood et al., 2007
Cu	5 μM $CuSO_4$	12 days	solution	*Arabidopsis thaliana*	Sofo et al., 2013
Fe	200 μM Fe-EDTA	15 days	agar	*Arabidopsis thaliana*	Giehl et al., 2012
Zn	10 μM $ZnSO_4$	3 days	solution	*Triticum aestivum*	Mahmood et al., 2007
Zn	50 μM $ZnSO_4$	7 days	solution	*Brassica juncea*, *Brassica napus*	Feigl et al., 2015
Zn	1000 mg kg^{-1} ZnO	42 days	soil in rhizobox	*Thlaspi caerulescens*	Whiting et al., 2000
Zn	400 μM $ZnCl_2$	4 or 10 days	solution	*Solanum nigrum*	Xu J et al., 2010a
Zn	150 μM $ZnSO_4$	12 days	solution	*Arabidopsis thaliana*	Sofo et al., 2013
Ni	75 μM $NiCl_2$	12 days	agar	*Arabidopsis thaliana*	Wang et al., 2015
Ocassionally essential elements					
Se	25 mg kg^{-1} Na_2SeO_3	79 days	soil in rhizobox	*Stanleya pinnata*	Goodson et al., 2003
Se	10 μM Na_2SeO_3	14 days	agar	*Arabidopsis thaliana*	Lehotai et al., 2012
Co	50 μM $CoCl_2$	4 days	solution	*Lycopersicon esculentum*	Xu S et al., 2010
Co	50 or 70 μM $CoCl_2$	12 days	agar	*Arabidopsis thaliana*	Wang et al., 2015
Co	10 or 20 μM $CoCl_2$	3 days	solution	*Oryza sativa*	Hsu et al., 2013
Al	50 μM $AlCl_3$	5 days	solution	*Zea mays*	Doncheva et al., 2005
Al	100 μM, 200 μM $AlCl_3$	4 days	agar	*Arabidopsis thaliana*	Illéš et al., 2006
Other essential elements					
Cr	500 μg ml^{-1} $CrCl_3$	–	solution	*Triticum aestivum*	Hasnain and Sabri, 1997
Cr (VI)	200 μM $K_2Cr_2O_7$	5 days	agar	*Arabidopsis thaliana*	Castro et al., 2007
Va	20-40-80 mg L^{-1} NH_4VO_3	7 days	solution	*Brassica campestris*	Vachirapatama et al., 2011
Non-essential elements					
Pb	10 μM $PbCl_2$	3 days	solution	*Oryza sativa*	Mahmood et al., 2007
Pb	10^{-3} M $PbNO_3$	3 days	solution	*Zea mays*	Obroucheva et al., 1998
Pb	1200 μM $PbNO_3$	12 days	agar	*Arabidopsis thaliana*	Wang et al., 2015
Cd	50 μM Cd	48 h	agar	*Arabidopsis thaliana*	Potters et al., 2007
Cd	50 μM $CdSO_4$	5 days	agar	*Arabidopsis thaliana*	Hu et al., 2013
Cd	10 μM $CdSO_4$	12 days	solution	*Arabidopsis thaliana*	Vitti et al., 2013; Sofo et al., 2013
Cd	25, 50, 75, 100 μM $CdCl_2$	5 days	agar	*Arabidopsis thaliana*	Li et al., 2016
As	25 μM As(III)	3 days	agar	*A. thaliana*	Krishnamurthy and Rathinasabapathi, 2013
Combination of elements					
Cd + Cu + Zn	10 μM $CdSO_4$ + 5 μM $CuSO_4$ + 150 μM $ZnSO_4$	12 days	solution	*Arabidopsis thaliana*	Sofo et al., 2013