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REVIEW

Nitric oxide as a potent signalling molecule in plants

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ABSTRACT The role of NO in stress responses in plants came in the focus of plant science in the last decade. Better understanding of plant stress responses is very important in the light of increasing intensities of stressors like drought, salinity and others, due to global climatic and environmental changes. Our knowledge, concerning signal transduction pathways is very scarce, especially in terms of NO-related alterations in proteins and gene expression as well as regulation. In this review we consider different NO-reactions, signalling pathways, NO – plant hormone interactions and NO-induced and -mediated signalization under osmotic stress in relation with the development of root architecture.

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A potent signalling molecule is supposed to be effective in fast responses to environmental or intracellular stimuli by increasing and decreasing its concentration, its reactions should be specific for the target molecules, and its appearance should be temporally and locally adequate. Nitric oxide seems to be a proper signalling molecule, although its sources and production, as well as the ways of its removal are not clearly understood in plants. Recently two reviews have been published covering these topics (Neill et al. 2008; Wilson et al. 2008), therefore in this present overlook we will consider different aspects of NO signalization under abiotic stress conditions and in root development.

Nitric oxide is a free radical, diffusible, lipophylic gas which has three forms in both animals and plants: NO^+ (nitrosonium cation), NO^- (nitroxyl anion) and $NO^{\cdot}$ (nitric oxide radical), often referred to as reactive nitrogen species (RNS) and nitrosative stress. The term RNS is not recognised widely in contrast to the term reactive oxygen species (ROS), though as distinct dynamic elements they were synthetized together with a third reactive family, the reactive sulphur species (RSS), by Yamasaki (2005).

Further RNS are the derivatives of S-nitrosylation and nitrosation reactions with thiol-contaning substances, especially reactive cysteine thiol moieties and iron-sulphur clusters, as well as with protein tyrosine residues (Espey et al. 2002; Wang et al. 2006; Corpas et al. 2007). In plants, probably the most frequent S-nitrosylated compound is S-nitrosoglutathione (GSNO) which serves as NO-donor to subsequent nitrosylation reactions. In *Arabidopsis*, a great number of S-nitrosylated proteins were identified like metabolic enzymes, proteins participating in photosynthesis and in redox reactions etc. (Lindermayr et al. 2005). Since these reactions are reversible (e.g. *in vitro* by using dithiotreitol, DTT), investigation of S-nitrosylated and nitrosated components may provide insight into NO-related signalling pathways.

Our previous experiments also show that NO is an active signal component in different stress responses like drought/osmotic stress and heavy metal load. Interestingly, the appearance of NO, as the function of time and spatial localization in roots, suggests different mechanisms involved in NO production and in the role of signal transduction (Bartha et al. 2005; Kolbert et al. 2005; Kolbert et al. 2008b). Thus, in the case of Cu^{2+} treatments of *Pisum sativum* and *Brassica juncea*, an early NO burst was obtained 2 h after subjecting the plants to the metal ions whereas fast NO-production did not appear after cadmium treatment (Bartha et al. 2005). The source of NO in this case may be GSNO, since copper can catalyze the decomposition of RS-NO by redox reaction (redox potential for Cu^{2+}/Cu^+, E_0 = +0.15 V) either by the one-electron reduction reaction by the monovalent species, or with the divalent copper, in the presence of oxidizer (Vanin and van Faassen 2007). Similar, but not identical reactions could be expected to occur by iron, however, the high redox potential for Fe^{3+}/Fe^{2+} (E_0 = 0.77 V) leads to the formation of low molecular weight dinitrosyl iron complexes (DNICs) which presence is also proved in plants. DNICs can serve as source and storage of NO and also participate in plant iron metabolism (Graziano and Lamattina 2007). In this way, the kinetics of early NO transients seem to depend on the source of NO. For instance, very early NO burst, developed in 30 min, was observed in response to Fe^{2+}-treatment in Arabidopsis, preceding *ATFer1D* gene expression (Arnaud et al. 2006), or, as mentioined before, in the case Cu^{2+} treatments of *Pisum sativum* and *Brassica juncea* (Bartha et al. 2005). In addition, these transition metal ions, in the Fenton reaction with H_2O_2, produce hydroxyl radicals leading to the formation other reactive oxygen species (ROS). Oxidative stress may

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involve NO as well playing a role in drought responses in the abscisic acid pathway in wheat root (Zhao et al. 2001).

Osmotic stress has two components, non-ionic osmotic and ionic strength. Both stressors evoke oxidative stress as well, and the close interaction between ROS and RNS is obvious. In one of our earlier papers we have been focussing on the co-stress responses in plants, including osmotic stress hormones like abscisic acid and ethylene – nitric interactions as well (Leshem et al. 1998). It is clear that the very different abiotic stressors like UV-B radiation (Barabás et al. 1998), salinity (Barabás et al. 2000; Rios-Gonzales et al. 2002), or heavy metals (Fediuc et al. 2002, 2005) all evoke oxidative stress and changes in antioxidant defence mechanisms.

Different reactive oxygen species, mainly the relative long-lived and diffusible H_2O_2 can also function as signalling molecule that mediate responses to different stresses (Vranová et al. 2002, Mittler et al. 2004). In plants, both NO and H_2O_2 generation are activated by several hormonal and environmental stimuli to trigger a range of cellular processes (Desikan et al. 2004). Data have suggested that NO serves to modulate H_2O_2 production and downregulate its effects on defence-related gene expression. In a number of responses, NO and H_2O_2 generation occur in parallel, or in a short succession of one another, and it had been shown that they can act both synergistically and independently (Delledonne et al. 2002; de Pinto et al. 2002; Bright el. 2006).

In addition to their defence-related roles, NO and H_2O_2 are important endogenous signals in many vital aspects of plant growth and development such as root growth, root gravitropism, xylogenesis and seed germination (Pagnussat et al. 2002; Hu et al. 2005; Bright et al. 2006).

Photosynthetic electron transport and related light-dependent enzyme activities are also targets of NO due to their thiol residues, transition metal components and iron-sulphur clusters. The role of nitric oxide (NO) in photosynthesis is, however, poorly understood as indicated by a number of studies in this field with often conflicting results. As various NO donors may be the primary source of discrepancies, in our recent study a set of NO donors and its scavengers were applied, and the effect of exogenous NO was examined on photosynthetic electron transport *in vivo* as determined by chlorophyll fluorescence of pea (*Pisum sativum*) leaves (Wodala et al. 2005, 2008). Sodium nitroprusside-induced changes were shown to be mediated partly by cyanide, and S-nitroso-N-acetylpenicillinamine provided low yields of NO. However, the effects of S-nitrosoglutathione were inferred exclusively by NO, which made it an ideal choice for this study. Q_A^- reoxidation kinetics showed that NO slowed down electron transfer between Q_A and Q_B, and inhibited charge recombination reactions of Q_A^- with the S_2 state of the water-oxidizing complex in photosystem II. Consistent with these results, chlorophyll fluorescence induction suggested that NO also inhibited steady-state photochemical and non-photochemical quenching processes. NO also appeared to modulate reaction-center-associated non-photochemical quenching.

Different signalling pathways

Recently, increasing attention is directed to the details of functional signalling pathways. It was an important observation, that NO stimulated cGMP formation in spruce needles (Pfeiffer et al. 1994). In addition, NO activates cGMP-dependent pathway leading to adventious root formation in cucumber (Pagnussat et al. 2003). Recently, the S-nitrosylation reactions of NO are emphasized besides the cGMP-related signalling pathway. In guard cells, outward-rectifying K^+ cannels seem to be directly controlled by nitrosylation (Sokolovsky and Blatt 2004), however, as shown by Distéfano et al. (2008) the process of stomatal closure involves NO-mediated phosphatidic acid accumulation with the implications of phospholipases C and D. A very significant consequence of this route that it connects to phospholipid signalling pathway.

Further evidence for the involvement S-nitrosylation reactions was published for cadmium stress in pea plants (Barroso et al. 2006) and for NaCl-salinity in olive leaves (Valderrama et al. 2007). In the first case the presence of GSNO and the expression of GSNO-reductase (GSNOR) was shown, in the latter case increased L-arginine dependent NO-production, enhanced level of total S-nitrosothiols and tyrosine nitration of different proteins were found. We note that the arginine-dependent nitric oxide production by nitric oxide synthase (NOS) is still a debated question in plants (Kolbert et al. 2008a and references therein). It has been reported that GSNOR is highly conservative among organisms (Liu et al., 2001), and glutathione-dependent enzyme formaldehyde dehydrogenase (FALDH 1.2.1.1) has been demonstrated to have GSNOR activity.

Several studies, based on plants with altered NO-levels, have recently provided genetic evidence for the importance of NO in gene induction. The activities of a variety of nuclear regulatory proteins are affected dramatically by NO. The formation of S-nitrosylated proteins seems to be an especially important mechanism in the regulation of the function/activity of transcription factors. S-nitrosylated proteins are created when a cysteine thiol reacts with NO in the presence of an electron acceptor to form an S-NO bond. Under physiological conditions this posttranslational modification affects the function of a wide range of cellular proteins, like stress-related proteins, signalling proteins, metabolic proteins, and nuclear regulatory proteins (Grün et al. 2006). In animals, *in vitro* activation of purified microsomal glutathione transferase 1 by S-nitrosylation has been reported. The activity of this enzyme is increased after treatment with N-ethylmaleinimide (NEM), a sulfhydryl alkylating reagent, and is also increased under conditions of oxidative stress. Preincubation of purified enzyme with GSNO or the nitric oxide donor, 1,1-diethyl-2-

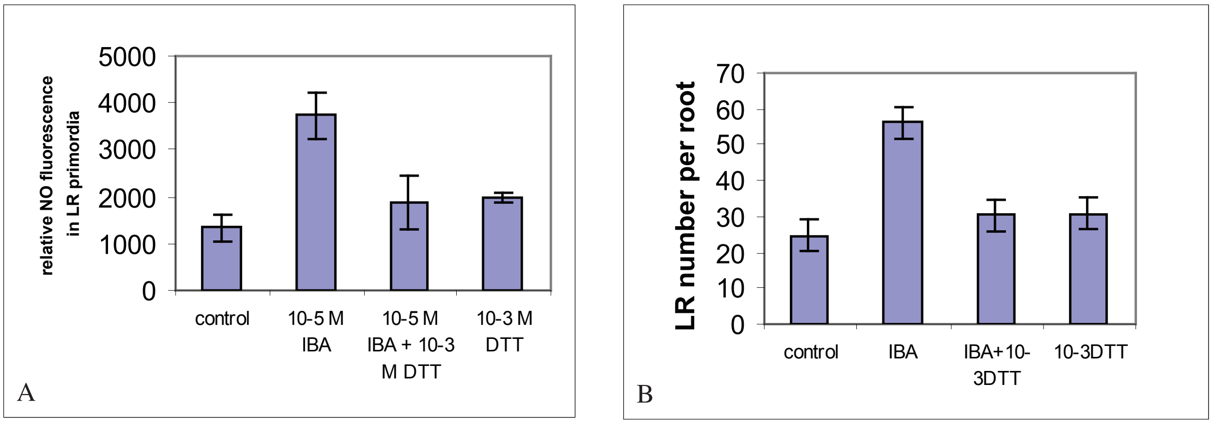

Figure 1. Dithiotreitol (DTT) in 10^{-3} M concentration reduced nitric oxide (NO) generation in lateral root primordia (A) and the exogenous auxin-induced lateral root (LR) induction (B).

hydroxy-2-nitrosohydrazine (DEA/NO), resulted in two-fold increase in enzyme activity (Ji et al. 2002). In *Arabidopsis*, one tau group glutathione S-transferase (GST) and one glutathione peroxidase (GPOX) enzymes proved to be target proteins of S-nitrosylation (Lindermayr et al. 2005). Both enzymes participate in glutathione dependent antioxidant defence pathways, thus involved in osmotic stress acclimatisation. GSTs have a role in the regeneration of S-thiolated proteins under oxidative stress (Basantani and Srivastava, 2007) and, according to the results of Kilili et al. (2004) they can be considered also as stress signal proteins.

The transcription of genes is controlled by transcription factors, however, their binding affinity to DNA or other proteins can be altered by modifications of their molecule by phosphorylation and S-nitrosylation. As discussed earlier, often different genes, involved in a particular mechanism, are co-regulated. This suggests the possibility for the existence of common transcription factor binding site in the promoter region of NO-responsive genes leading to their co-expression or co-regulation. By screening the promoter regions of such genes, in *Arabidopsis*, a large number of genes were found to be induced, up-regulated or down-regulated in response to NO treatments (Palmieri et al. 2008).

Interaction of NO with plant hormones

Interaction of NO with different plant hormones is also an intriguing area which is related to both developmental processes and stress responses.

Recently, it was suggested that stress-induced morphogenetic responses are controlled by auxin distribution in the plant (Potters et al. 2007). The question arose if there are similarities or differences in growth responses of a root system under external auxin load and osmotic stress, with focus on the role of NO in the phenotypic acclimation processes. Lateral roots are formed in the root pericycle postembryonically from specially positioned cells allowing broad phenotypic plasticity during further growth and development. The frequency of initiation of lateral roots is in part, determined by the auxin concentration: exogenous application of auxin increases the number of lateral roots. Recently it was shown that indole-3-butyric acid (IBA), a natural auxin besides the major indole-3-acetic acid (IAA), is involved in root formation especially in case of adventitious rooting from stem tissue (Ludwig-Müller et al. 2005). Earlier it was reported that the activity of IBA synthetase is enhanced by osmotic stress as well as by hormones involved in stress responses (Ludwig-Müller et al. 1995). In our recent study, the production of NO was investigated in the processes of indole-3-butyric acid (IBA)-induced lateral root (LR) initiation and primary root elongation as compared to those under osmotic stress conditions. Using IBA and polyethylene glycol as osmotic agent in broad concentration range during the time period of stress response, as well as NO scavenger agent, different roles of NO could be distinguished under these conditions (Kolbert et al. 2008b). Time-dependent properties of rooting processes and NO generation (Kolbert et al. 2008b) showed similarities between the two phenomena, *i.e.* the effect of 10^{-5} M IBA on lateral root number and NO fluorescence appeared after 48-hour treatment in both cases. The similar temporal formation of auxin- induced NO synthesis and LR initiation suggested a functional relation between these processes which hypothesis was confirmed by the result that NO fluorescence was strongly linked to auxin level in roots.

During osmotic stress, however, the time dependence of nitric oxide development showed significant difference as compared to that of IBA-treated roots, since the appearance of lateral initials was preceded by a transient burst of NO. This early phase of NO generation under osmotic stress, culminating at 24 h, was clearly distinguishable from that which accompanied LR initiation under both osmotic and

IBA treatments. The source and the role of this NO transient are certainly different from those of the constant and steady NO phase, which start after 48 hours of the treatments, when the transient one already has decayed. When the osmotic stress-induced NO burst was eliminated by the NO-scavenger cPTIO, less LRs were formed than in control and osmotic stressed roots, indicating that the early NO burst ("stress-NO") is necessary for the osmotic stress-induced lateral root formation. The role of NO in auxin-mediated activation of cell division and embryogenic cell formation was pointed out earlier by Ötvös et al. (2005). Our preliminary results indicate that in the LR formation S-nitrosylated signalization takes place, since under reducing environment (in the presence of DTT, Cleland 1964) both NO production and LR development were hindered in pea plants (Fig. 1AB.). It has to be mentioned that although DTT may influence many target proteins, however, its effect is not universally inhibitory (Chen and Qi 2007).

Taken together, literature data and our latest results refer to the different sources and localization of NO in the signal transduction pathways, i.e. it seems that NO is signalling in the early steps in stress responses followed by post-translational modifications of proteins, finally leading to gene regulation (Durner et al. 1998; Grün et al. 2006; Serpa et al. 2007).

Conclusion

Both environmental and endogenous factors influence the development of root architecture (Zhang et al. 1999; Malamy 2005; Malamy and Ryan 2001). Interplay between plant hormones like auxin, cytokinins and signalling substances, e.g. nitric oxide (NO), determine the growth of primary roots and initiation of lateral roots (Malamy and Benfey 1997; Correa-Aragunde et al. 2004; Kolbert et al. 2005). Stress-induced morphogenetic responses, in general, are controlled by auxin distribution in the plant and reactive oxygen species are part of the signalization between the stress and the morphogenetic response (Potters et al. 2007). Since the signalling pathways of ROS and RNS may interplay, the early appearance of the NO transient can be enrolled into the signal transduction pathway towards an altered root architecture which has significance in the phenotypic adaptation under drought conditions.

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